Received: 21 April 2022 | Accepted: 3 August 2022
DOI: 10.1002/hbm.26049

RESEARCH ARTICLE

WILEY

When action prediction grows old: An fMRI study

Lucia Maria Sacheli[1] | **Chiara Verga**[1,2] | **Laura Zapparoli**[1,3] | **Silvia Seghezzi**[1] | **Giulia Tomasetig**[1] | **Giuseppe Banfi**[3,4] | **Eraldo Paulesu**[1,3]

[1]Psychology Department and Milan Center for Neuroscience, University of Milano-Bicocca, Milan, Italy
[2]Department of Psychology, Faculty of Medicine and Psychology, Sapienza University of Rome, Rome, Italy
[3]IRCCS Istituto Ortopedico Galeazzi, Milan, Italy
[4]San Raffaele Vita e Salute University, Milan, Italy

Correspondence
Lucia Maria Sacheli and Eraldo Paulesu, Department of Psychology, University of Milano-Bicocca, Milano, Italy.
Email: lucia.sacheli@unimib.it and eraldo.paulesu@unimib.it

Funding information
Ministero della Salute, Grant/Award Number: RicercaCorrente; Ministero dell'Istruzione, dell'Università e della Ricerca, Grant/Award Numbers: 2017-NAZ-0435, CUP H45J170006300069; Milan Center for Neuroscience

Abstract

Predicting the unfolding of others' actions (*action prediction*) is crucial for successfully navigating the social world and interacting efficiently. Age-related changes in this domain have remained largely unexplored, especially for predictions regarding simple gestures and independent of contextual information or motor expertise. Here, we evaluated whether healthy aging impacts the neurophysiological processes recruited to anticipate, from the observation of implied-motion postures, the correct conclusion of simple grasping and pointing actions. A color-discrimination task served as a control condition to assess the specificity of the age-related effects. Older adults showed reduced efficiency in performance that was yet not specific to the action prediction task. Nevertheless, fMRI results revealed task-specific age-related differences: while both groups showed stronger recruitment of the lateral occipito-temporal cortex bilaterally during the action prediction than the control task, the younger participants additionally showed a higher bilateral engagement of parietal regions. Importantly, in both groups, the recruitment of visuo-motor processes in the right posterior parietal cortex was a predictor of good performance. These results support the hypothesis of decreased involvement of sensorimotor processes in cognitive tasks when processing action- and body-related stimuli in healthy aging. These results have implications for social interaction, which requires the fast reading of others' gestures.

KEYWORDS
action prediction, aging, fMRI, lateral occipito-temporal cortex

1 | INTRODUCTION

Successful interactions imply the ability to online read what other people are doing to predict the unfolding of their actions and plan an appropriate response. This anticipatory coding of others' gestures is crucial in both cooperative and competitive contexts, like during the performance of musical ensembles (Keller et al., 2014; Novembre et al., 2012, 2014; Novembre & Keller, 2014) or sport competitions (Aglioti et al., 2008; Makris & Urgesi, 2015; Tomeo et al., 2013; Urgesi et al., 2012): in these circumstances, flexible and fine-tuned temporal coordination engages not only visual but also motor processes.

It is widely accepted that motor representations of actions and their sensory consequences are encoded in the sensorimotor system independently of the specific task performed by the agent (e.g., action

---

Lucia Maria Sacheli and Chiara Verga contributed equally to this study.

observation, motor imagery, or action execution; Hommel et al., 2001; Jeannerod, 2001; Prinz, 1997). In primates, these tasks are associated with neural activity in specific premotor and parietal "mirror neurons" (Rizzolatti & Sinigaglia, 2016), which respond not only when performing but also when observing hand-object interactions, even when the action conclusion is hidden from view (Umiltà et al., 2001). In humans, homologous fronto-parietal areas support similar "mirror" mechanisms during action observation (Chong et al., 2008; Kilner et al., 2009; Mukamel et al., 2010). Previous neuroimaging and neurostimulation studies have shown that predicting the unfolding of observed actions (*action prediction* abilities) depends on the same fronto-parietal visuomotor network (Avenanti et al., 2018; Stadler et al., 2012; Urgesi et al., 2010; see also Kilner, 2011). For instance, the neuromodulation study by Avenanti et al. (2018) has demonstrated the causal role of the left premotor cortex in predicting the conclusion of human grasping actions. Together with the interconnected posterior parietal regions (Binkofski & Buccino, 2018; Blakemore & Sirigu, 2003; Tunik et al., 2007), these brain areas constitute a sensorimotor action observation network (AON, Grafton, 2009) responsible for predicting the unfolding of others' actions and their sensory consequences. These predictions are supported by internal models that link a stimulus (e.g., an observed movement) with its most likely conclusion and outcome, thanks to expectations based on prior experience (Friston et al., 2011; Kilner et al., 2007; Wolpert et al., 2003).

The question that we address in this article is whether these motor-cognitive mechanisms reorganize during early nonpathological aging.

Previous studies have shown an overall age-related decline in motor control. It leads to slowdowns of motor performance and a decreased smoothness in fine coordination (Buckles, 1993; Seidler, 2006; Seidler et al., 2010). These deficits in motor control are paralleled by a well-established age-related structural and functional neurophysiological decline, especially in the connectivity of fronto-parietal areas (Carp et al., 2011; Mattay et al., 2002; Ren et al., 2013; Seidler et al., 2010). The age-related decline also involves cognitive motor processes, such as motor imagery, with a lower temporal correlation between imagined and executed movement in older individuals (Personnier et al., 2008; Skoura et al., 2005), less vivid imagery, especially when imagining complex actions (Saimpont et al., 2013; Zapparoli et al., 2019), and a lower reliance on kinesthetic features in favor of visually based strategies (Zapparoli et al., 2013, 2016). Altogether, these results suggest that all motor-related processes, including reading online the movements of others, might be susceptible to detriment with aging. Within this line, some authors hypothesize that aging might determine a *reduced embodiment*, that is, a reduced involvement of sensorimotor processes in cognitive tasks (Costello & Bloesch, 2017; Kuehn et al., 2018). However, this is to date a mostly unexplored hypothesis in the domain of action prediction.

Concerning action observation, previous studies suggest that aging results in a less accurate ability to decipher the temporal unfolding of someone else's whole-body actions (Diersch et al., 2012, 2013), accompanied by changes in brain functioning. Diersch et al. (2013) found that older participants over-activate visual cortices to judge the temporal progression of complex action sequences observed in the far extra-personal space (e.g., figure skating elements or everyday actions like preparing the laundry). They concluded that older adults preferably adopt visual rather than motor strategies during this task, in line with the *reduced embodiment in aging* hypothesis (Costello & Bloesch, 2017; Kuehn et al., 2018). In sharp contrast with this conclusion, however, a previous study by Nedelko et al. (2010) provided evidence for a preserved functioning of the AON in older adults. In their study, the authors showed that the ventrolateral premotor cortex and the inferior parietal cortex, crucial nodes in the AON, do not exhibit activity changes as a function of age during motor imagery and action observation tasks. The authors interpreted the lack of age-related changes in these activations as evidence for the older participants' preserved functioning of sensorimotor processes during such cognitive tasks. More recently, Di Tella et al. (2021) expanded these findings by showing that older adults might show the coupling of structural and functional changes in the AON: they found that a reduced cortical thickness was coupled with a (possibly compensatory) increased activation of the premotor cortices bilaterally during action observation. Altogether (see also Farina et al., 2017), these findings suggest that older adults might still engage sensorimotor processes supported by the AON during action observation. As an aside, this evidence provides a rationale for applying action-observation protocols to the rehabilitation of motor disorders in older populations like neurological patients (Buccino, 2014).

However, the scarce and controversial evidence reported above leaves us with an open question: the visuo-motor processes sustained by the AON should be considered exceptionally resistant to age-related decay (see Di Tella et al., 2021; Farina et al., 2017; Nedelko et al., 2010) or one of those most subjected to functional reorganization, as suggested by the *reduced embodiment in aging* hypothesis (Costello & Bloesch, 2017; Kuehn et al., 2018)?

Here, we aimed to address this issue by focusing on action prediction, a rather unexplored field in the literature on aging. Importantly, action prediction tasks are slightly different from mere action observation because they imply the active use of motor representations to anticipate the unfolding of observed actions. The only available studies in this domain (Diersch et al., 2012, 2013, 2016) focused on the role of expertise and familiarity in modulating the older adults' capacity to monitor complex action sequences (figure skating elements or everyday actions like preparing the laundry) and lacked a control task that could make the result interpretation straightforward. Thus, the question remains: does a task-specific impact of nonpathological early aging exists when older individuals have to decipher the kinematics of simpler gestures and predict their conclusion? Previous work has shown the activation of the AON in older participants during passive observation of object grasping (Di Tella et al., 2021; Farina et al., 2017; Nedelko et al., 2010). Would they also take advantage of this network when predicting the conclusion of similar actions? Given the relevance of action prediction for the ability to interact effectively with conspecifics (Bekkering et al., 2009; Candidi et al., 2015; Knoblich & Jordan, 2003; Pecenka & Keller, 2011; Sacheli et al., 2018a, 2018b), answering this question would critically contribute to the understanding of age-related changes in the capacity of navigating the social world and its sensorimotor roots.

In this study, we thus aimed to investigate whether the visuomotor mechanisms involved in action prediction and supported by neural activity in the AON degrade with aging. To avoid the confound of expertise, we concentrated on the observation of overlearned movements (grasping and pointing) performed by a potentially interacting partner who reached for a simple cubed-shaped object placed in the (virtual) peri-personal space of the observer. Younger and older participants were required to predict the conclusion of these grasping and pointing movements presented at mid-flight (i.e., during action unfolding) by implied-motion pictures and then judged whether the following picture depicted the correct conclusion. Implied-motion images proved to induce a robust sensorimotor simulation in young, healthy participants (Avenanti et al., 2013; Urgesi et al., 2010): we employed these stimuli as they do not require subtle discrimination of temporal features and minimize the visual complexity as well as the impact of contextual information. Upper limb gestures observed in peri-personal space may involve a potentially better engrained and less vulnerable mechanism than what was previously observed for complex visual stimuli (as those employed by Diersch et al., 2012, 2013, 2016). From previous primate and human data (Hardwick et al., 2018; Rizzolatti & Sinigaglia, 2016), we anticipated the involvement of a vast fronto-temporoparietal network in younger participants during the task. We aimed to test whether older adults recruit the same neural resources and the association of possible age-related differences with individuals' performance at the task.

Differently from previous attempts (Diersch et al., 2012, 2013; Diersch et al., 2016), the task-specificity of the results was ensured by the addition of a control, color-discrimination task: this allowed us to test whether potential group differences in performance were specific to action prediction or generalized to other visual tasks having a similar structure but lacking the crucial element of action prediction.

Although we designed the study to challenge the hypothesis of a *reduced embodiment in aging* (Costello & Bloesch, 2017; Kuehn et al., 2018) and we were mainly interested in the visuo-motor processing occurring in the AON, all neurofunctional analyses were unconstrained and performed at the whole-brain level. This made our quest not constrained by a priori-assumption allowing us to detect, if any, evidence for alternative hypotheses as well. More specifically, we tested whether (possible) age-related neurofunctional changes during action prediction occur within the nodes of the AON or in regions outside this brain network, like prefrontal ones, as predicted by the classical theories of cognitive aging (see Davis et al., 2008). Based on recent evidence from our lab derived from motor imagery tasks, age-related changes were expected in the parietal cortex (Zapparoli et al., 2019), paralleled by a greater reliance on visual processing (Zapparoli et al., 2013, 2016).

To sum up, our experimental design allowed us to assess: (i) possible age-related changes in performance that were specific to the action prediction (as compared to a control) task, and (ii) their association with possible neurophysiological changes. While the *reduced embodiment in aging* hypothesis would predict either a performance decay specific to action prediction or a preserved performance sustained by compensatory brain activations outside the AON, an alternative view would expect compensatory brain activations within the AON and especially reliant on premotor activations, in line with some previous studies on action observation in aging (Di Tella et al., 2021; Farina et al., 2017; Nedelko et al., 2010). Importantly, what counts to us is that our experimental paradigm was sufficiently sensitive to show, in younger participants, the involvement of the AON, which should be specific to the action prediction (as compared to the control) task and functional to the behavioral performance: this would be the proof of concept to assume that any group-specific difference is not a mere by-product of a nonsensitive experimental design.

2 | MATERIALS AND METHODS

2.1 | Participants

Twenty younger (8 females, age range 19–27 years, mean age 23.20 ± 1.77 years) and twenty older healthy participants (10 females, age range 56–72 years, mean age 62.60 ± 4.76 years), all with high education (younger group, median [Me] = 16 years, range 18–13 years; older group Me = 16 years, range 19–8 years; Mann–Whitney *U* test = 154.5, $p = .204$), took part in the study. All the participants were right-handed, reported normal or corrected-to-normal vision, and were naive as to the purpose of the experiment. The participants' enrollment was inclusive of all persons without limitations by gender or ethnicity. Inclusion criteria required the absence of major neurological and psychiatric disease and of physical limitations that could restrain the participants' upper-limb mobility. Older participants were also screened to exclude age-related neurocognitive decay by using the Mini-Mental State Examination (MMSE) of general cognitive functioning (Measso et al., 1993), the Raven's progressive matrices measuring nonverbal logical reasoning (Basso et al., 1987), the digit span forward and backward (Orsini et al., 1987) assessing verbal short-term memory and working memory, and the frontal assessment battery (FAB, Appollonio et al., 2005). No participant showed pathological performance at the neuropsychological tests after correcting the scores for age and education (MMSE corrected score, Me = 27.92, range 30–25.46; Raven's corrected score, Me = 34.5, range 36–26.5; digit span forward corrected score, Me = 5.75, range 8.75–4.5; digit span backward corrected score Me = 4.87, range 7.97–2.87; FAB corrected score Me = 18, range 18–16).

The experimental protocol was approved by the Ethics Committee of the IRCCS Istituto Ortopedico Galeazzi (Comitato Etico dell'Ospedale San Raffaele di Milano) where data collection took place. All participants gave their written, informed consent to take part in the study, following the ethical standards of the 1964 Declaration of Helsinki and later amendments, and were debriefed as to the purposes of the study at the end of the experimental procedures.

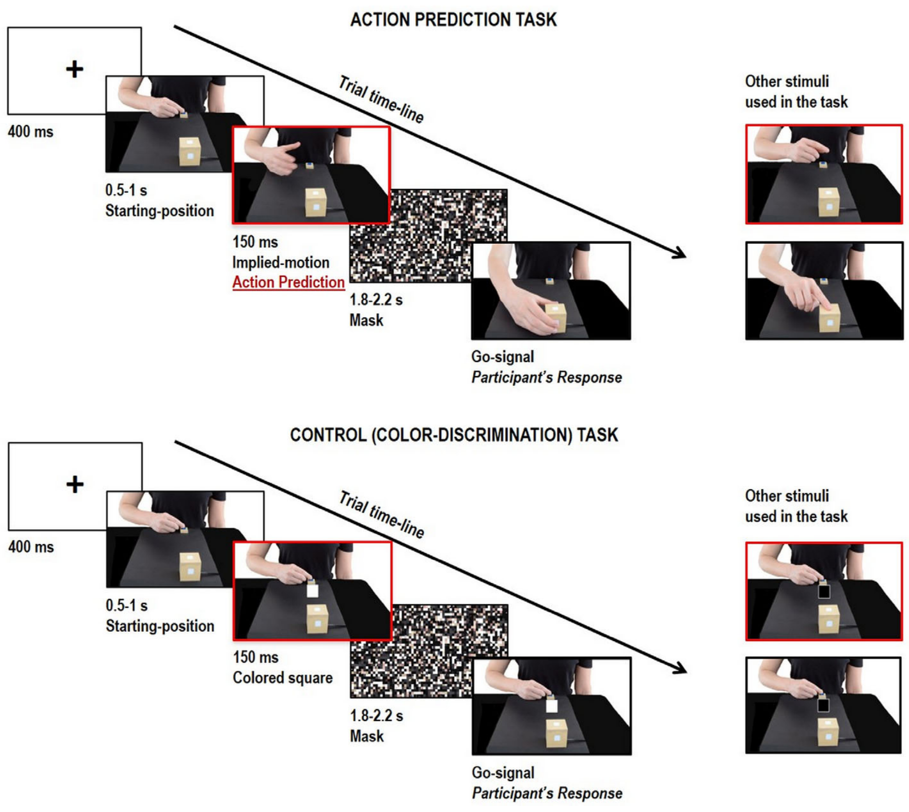

FIGURE 1 The figure illustrates the trial-time line, which was identical in the action prediction (upper panel) and the control (lower panel) tasks. The only difference between the two tasks resided in the implied-motion image, which was substituted by an image including the colored square (black or white) in the control task. After the go-signal, the participants were required to decide whether the last image correctly concluded the movement previously seen (action prediction task) or matched with the previously seen colored square (control task). The red frames indicate the onset of the event of interest in the fMRI analyses.

2.2 | Familiarization phase and neuropsychological assessment

Before the fMRI session (2–4 days before), all the participants were screened for contraindication to fMRI and underwent a brief learning phase (including sixteen trials, eight per task) to familiarize with the visual stimuli and the experimental setup. During the same session, the older participants were assessed with the neuropsychological tests.

2.3 | Experimental design

2.3.1 | Stimuli and apparatus

During the experimental condition (*action prediction*), the participants observed visual stimuli consisting of a set of pictures showing the trunk and upper limbs of a human actor in different positions (see Figure 1, *upper panel*): (i) a starting-position image, (ii) an implied-motion image (depicting the pointing/grasping actions at mid-flight), and (iii) an end-position image (depicting the end of the pointing/grasping action). To enhance variability, the implied-motion image depicted the movement at different time-points, namely at 1/6, 1/4, and 1/3 of total movement duration. A scrambled version of each of the implied-motion images was shown during the task as a mask (between the presentation of the implied-motion and the final-position images, see Figure 1).

As a *control* condition, the participants performed a color discrimination task. In this case, the implied-motion and end-position images were replaced by the repetition of starting-position images, where a black or white colored square was added in the middle of the picture (Figure 1, *lower panel*).

We designed the control condition in order to assure that the potential differences between the two groups were not due to a generalized age-related decrease in response speed (see Nebes, 1978). A similar approach was applied in our previous studies on aging and motor cognition (Zapparoli et al., 2016, 2019). The choice of this particular control task was dictated by the desire of engaging the participants with stimuli that maintained constant the target (cube-shaped) object and the presence of a human body, allowing us to control for perceptual differences between the two tasks.

Visual stimuli were delivered using VisuaStim fiber-optic goggles (800 × 600 pixel resolution). Responses were recorded through an MRI-compatible response-box (Resonance Technology Inc., Northridge, CA) placed under the right hand of the participant lying in the scanner. Participants were instructed to respond by pressing a button either with the index or the middle finger.

2.3.2 | Procedure and trial-time line

The fMRI run was divided into four action prediction and four control blocks, administered in counterbalanced order between the participants. Although visual stimuli differed between the two experimental conditions, the trial timeline was identical (see Figure 1).

Each trial started with a fixation-cross displayed on the screen (400 ms), followed by the presentation of the starting-position image (variable stimulus duration ranging from 500 to 1000 ms). The variable duration of stimuli generated a desirable jittering in the onsets used for the fMRI data analyses. After that, in the *action prediction* condition, the implied-motion image was shown (duration 150 ms), followed by a scrambled image that served as mask (variable duration between 1800 and 2200 ms). Finally, the end-position image was shown, and the participants had to determine whether the end position-image *matched or not with the conclusion of the action* previously shown by the implied-motion image.

Responses were provided by pressing a button with either the index or middle finger (maximum response time [RT] allowed 2500 ms). In the color discrimination *control* task, the trial-timeline was identical, but the implied-motion and end-position images were replaced by starting-position images containing a black or white colored square. In this case, the participants were asked to determine whether the color of the square presented after the mask correctly matched with the color of the square presented before the mask. In all the experimental conditions, the participants were told to respond as quickly and correctly as possible.

While lying in the scanner, the participants first tried out the task (eight-trial practice block) and then started the fMRI session.

Stimuli presentation and randomization were controlled by E-Prime2 software (Psychology Software Tools Inc.).

2.3.3 | Block structure

Each of the four action prediction and four control blocks comprised of 12 trials. Overall, the participants performed 48 trials per experimental condition (corresponding to 96 trials for the whole session, for a total duration of ~11 min). Within each block, in random order, the participants observed 50% of grasping/pointing gestures (action prediction task) and 50% of black/white colored squares (control task). The number of times the participants observed the implied-motion image depicting the movement at each time-point (1/6, 1/4, and 1/3 of the total movement duration) was also balanced within each block. To create variability within the task and force participants to generate predictions when observing the implied-motion picture, the final picture correctly concluded the action (action prediction task) or matched with the previously observed color (control task) in the 50% of the trials.

2.4 | Behavioral data statistical analyses

The aim of the study was to investigate possible group differences (younger vs. older group) in the two tasks (action prediction vs. control task) to assess possible age-related changes in performance that were specific to the action prediction task. We collected the following behavioral indexes: (i) the sensitivity (d') as measured in accordance with the signal detection theory (Stanislaw & Todorov, 1999); (ii) the accuracy (ACC), that is, the proportion of correct responses; and (iii) the RTs, that is, the time-delay between the onset of the end-position image (or of the second image showing the colored square in the control task), which constituted the participants' go-signal, and the instant the participant pressed the response button, as measured in correct trials only. To obtain a measure that appropriately weighs the impact of speed and accuracy thus controlling for speed-accuracy trade-offs, we then calculated the Inverse Efficiency Score (IESs, Bruyer & Brysbaert, 2011), that is, the RTs/ACC ratio.

To calculate the sensitivity (d'), we subtracted the z-transformed false alarm (F) rate from the z-transformed Hit (H) rate [$d' = z(H) - z(F)$]; we considered as "hits" the "yes" responses provided in the trials where the final picture correctly completed the implied-motion picture (action prediction task) and the color matched with the one observed before the mask (control task), and "false alarms" the "yes" responses provided in trials where it was not the case.

To calculate the IESs, we calculated the individual ACC and mean RTs in each task (action prediction and control), excluding from the analysis of RTs any outlier value that fell 2.5 SDs above or below the individual's mean for each experimental condition. We calculated the IES for each participant, separately in each task (action prediction and control) to obtain a measure that captures participants' performance as a whole. For the sake of clarity, the separate analysis of the ACC and RTs is reported in the Supporting Information.

Both sensitivity (d') and the IESs were normally distributed according to the Kolmogorov–Smirnov test (all *ps* > .1). They were entered in a 2 × 2 ANOVA with group (younger vs. older adults) as between-subject factor and task (action prediction vs. control) as within-subject factor. Post hoc test applied the Bonferroni correction when needed.

All inferential tests of significance were based upon an α level of .05. Data were analyzed with the statistical software jamovi [The jamovi project (2021). jamovi (Version 1.6) [Computer Software]. Retrieved from https://www.jamovi.org].

2.5 | MRI data acquisition and analyses

2.5.1 | Data acquisition

MRI scans were acquired using a Siemens Magnetom Avanto 1.5 T scanner (Siemens AG, Erlangen, Germany) equipped with gradient-echo echo-planar imaging (EPI) (repetition time [TR] 2150 ms, echo time [TE] 40 ms, flip angle 90°, 28 slices, slice thickness 4 mm, interleaved slice acquisition, matrix 64 × 64, FOV 250 × 250 mm). Overall, 300 scans per run were acquired. The first two volumes recorded from each functional run were removed to allow for steady-state tissue magnetization. MPRAGE high-resolution T1-weighted structural images were also acquired (flip angle 35°, TE 5 ms, TR 21 ms, FOV 256 × 192 mm, matrix 256 × 256, TI 768, for a total of 160 axial slices with 1 × 1 × 1 mm voxels).

2.5.2 | Preprocessing

After image reconstruction, raw data visualization and conversion from the DICOM to the NIfTI format were performed with MRIcron (www.mricro.com) software. All subsequent data analyses were performed in MATLAB R2019b (MathWorks) using Statistical Parametric Mapping software (SPM12, Wellcome Department of Imaging Neuroscience, London, UK). First, slice-timing correction as implemented in SPM12 was applied. Then, the fMRI scans were realigned and unwarped to account for any movement during the experiment; the unwarped images were stereotactically normalized into the SPM12 template (EPI.nii) using the old normalization procedure to allow for group analysis of the data. At this stage, the data matrix was interpolated to produce voxels 2 × 2 × 2 mm in dimension. The stereotactically normalized scans were smoothed using a Gaussian filter of 10 × 10 × 10 mm to improve the signal-to-noise ratio and make the family-wise error rate (FWER) cluster-level correction applicable to the group-level analyses (Flandin & Friston, 2019).

Artifact detection tools (Whitfield-Gabrieli, http://www.nitrc.org/projects/artifact_detect) was used to identify outlier scans in global signal and movement for each participant. Time-points were marked as outliers when scan-to-scan variations in the global signal exceeded 9 SD from the mean, and when the compounded measure of movement parameters exceeded 2 mm scan-to-scan movement. On average, excluded volumes were 0.25 ± 0.77% in younger participants, and 1.54 ± 2.70% in older participants. Outlier scans were excluded from the single-subject analysis. No participant was excluded from the analysis for excessive movement, as established by the threshold of 20% of outlier scans in the fMRI run.

2.5.3 | Statistical analyses of the fMRI data

A two-step statistical analysis, based on the general linear model, was performed. At the first level of analysis (single-subject level), the blood oxygen level-dependent (BOLD) signal associated with each experimental condition was analyzed by convolution with a canonical hemodynamic response function (Worsley & Friston, 1995). Global differences in the fMRI signal were removed from all voxels with grand mean scaling. The time series was high-pass filtered at 128 s and pre-whitened by means of an autoregressive model AR(1) to remove artifactual contributions to the fMRI signal, such as noise from cardiac and respiratory cycles.

A fixed-effect analysis was performed, in which condition-specific effects were calculated in each participant. In an event-related design, the event duration was set to 0 s, and the onset of the event at each trial corresponded to the onset of the image following the starting-position one: in the action prediction task, it corresponded to the onset of the implied-motion image, while in the control task it corresponded to the onset of the first image with the colored-square (Figure 1, red frames). This time-point was characterized by the requirement to keep in mind the predicted action conclusion (action prediction task) or the color of the square (control task) until the mask off-set. Only in the action prediction task, however, the selected time-point also implicitly required to predict the conclusion of the observed action.

Separate regressors also modeled experimental confounds, including (i) the signal associated with the preparation of the motor response (the go-signal time-point at each trial, see Figure 1), (ii) trials in which the participants provided a wrong response (accuracy = 0) or RTs were outlier values, and (iii) the realigning parameters calculated in the preprocessing step. For each participant, we calculated the linear contrast "action prediction > control task" because we aimed to explore age-related differences in the task-specific neural correlates of action prediction while controlling for perceptual processes and the requirement to keep in mind a relevant piece of information (i.e., the predicted action conclusion in the action prediction task, or the color of the square in the control task).

At the second level of analysis (group-level analysis), we performed an independent-sample *t* test to explore age-related differences and communalities in the neural responses. For the sake of clarity, we also report in the Supporting Information the results associated with the simple effect of interest ("action prediction > control task") in each group. We also planned to extract the individual values associated with these effects and explore their parametric association with the behavioral performance shown by the participants at the action prediction (as compared to the control) task.

All fMRI data analyses were conducted at the whole-brain level. All the reported results apply an FWER correction for multiple comparisons at the cluster-level. The cluster-wise correction was applied to data having applied a 10 × 10 × 10 Gaussian smoothing and at $p < .001_{\text{uncorr}}$ at the voxel-level, as recommended by Flandin and Friston (2019). Regional effects that also met an FWER-correction at the voxel-level are reported in Table 2 and Supplementary Tables S1 and S2.

3 | RESULTS

3.1 | Behavioral results

Descriptive statistics are reported in Table 1.

3.1.1 | Sensitivity (d')

The ANOVA showed a significant main effect of the task ($F(1,38) = 6.17$, $p = .018$, $\eta_p^2 = .14$), indicating that the sensitivity was higher in the control than the action prediction task in all participants (action prediction task mean $d' = 2.76 \pm 0.99$; control task mean $d' = 3.16 \pm 0.69$). The results also showed a significant main effect of the group ($F(1,38) = 10.97$, $p = .002$, $\eta_p^2 = .22$), indicating that the sensitivity was higher in younger than older participants (younger group mean $d' = 3.28 \pm 0.50$; older group mean $d' = 2.64 \pm 0.70$). The group by task interaction was not significant ($F(1,38) = 0.001$, $p = .970$, $\eta_p^2 < 0.01$), indicating that the reduction in sensitivity in the

TABLE 1 Descriptive statistics of the behavioral data (younger adults, $N = 20$, older adults, $N = 20$)

		Younger adults		Older adults	
		Action prediction	Control task	Action prediction	Control task
d′	M	3.08	3.48	2.44	2.85
	SD	0.84	0.55	1.05	0.68
Accuracy	M	0.93	0.97	0.87	0.92
	SD	0.06	0.03	1.22	0.06
RT (ms)	M	688.09	606.84	956.36	918.92
	SD	113.15	108.04	153.83	157.29
IES (RT/ACC)	M	743.57	627.89	1129.01	1006.01
	SD	148.81	114.60	297.85	216.11

TABLE 2 Group comparisons of the neurofunctional results; (a) conjunction analysis (younger ∩ older adults), and (b) "younger > older adults" differences in the "action prediction > control task" contrast (younger adults, $N = 20$, older adults, $N = 20$)

a. Younger ∩ older adults	Left hemisphere				Right hemisphere			
Brain area (Brodmann area)	*X*	*Y*	*Z*	Z-score	*X*	*Y*	*Z*	Z-score
	Left occipito-temporal cluster $k = 634$, $p_{\text{FWER-corr}} < .001$				Right middle temporal cluster $k = 446$, $p_{\text{FWER-corr}} < .001$			
Middle temporal gyrus (37)	−52	−66	6	4.7	54	−62	4	4.8*
	−56	−68	8	4.5	50	−68	0	4.5
	–	–	–	–	50	−72	2	4.4
	–	–	–	–	44	−68	0	4.3
Middle occipital gyrus (19/37)	−46	−70	4	4.3	–	–	–	–
	−44	−72	6	4.0	–	–	–	–
	−44	−76	8	3.8	–	–	–	–
	−44	−78	12	3.8	–	–	–	–
	−38	−74	2	3.2	–	–	–	–
Inferior occipital/temporal gyrus (37)	−50	−68	−4	4.2	–	–	–	–

b. Younger > older adults	Left hemisphere				Right hemisphere			
Brain area (Brodmann area)	*X*	*Y*	*Z*	Z-score	*X*	*Y*	*Z*	Z-score
	Left parietal cluster $k = 206$, $p_{\text{FWER-corr}} = .011$				Right parietal cluster $k = 149$, $p_{\text{FWER-corr}} = .045$			
Postcentral gyrus (2)	−44	−36	60	4.1	36	−46	68	3.7
	−44	−38	64	4.0	36	−42	66	3.4
	−38	−38	68	3.8	34	−40	58	3.3
	Cluster in the left precuneus $k = 453$, $p_{\text{FWER-corr}} <.001$							
Superior parietal lobule (7)	−18	−82	52	3.9	36	−50	70	3.8
Inferior parietal lobule (40)	–	–	–	–	38	−44	58	3.4
	–	–	–	–	40	−48	58	3.4
	–	–	–	–	40	−40	52	3.5
	–	–	–	–	44	−36	52	3.3
Precuneus (7)	−6	−74	56	4.5	–	–	–	–
	−2	−76	52	4.2	–	–	–	–

Note: *X*, *Y*, and *Z* are the stereotactic coordinates of the activations in the MNI space. All reported voxels ($p < .001_{\text{uncorr}}$) are included in clusters surviving the FWER correction at the cluster-level. A maximum of 16 coordinates (local maxima) per cluster has been reported, each placed at least 4 mm apart, as reported by default in SPM12. (*) Z-scores statistically significant also after FWER correction at the voxel-level.

Abbreviations: FWER, family-wise error rate; MNI, Montreal Neurological Institute.

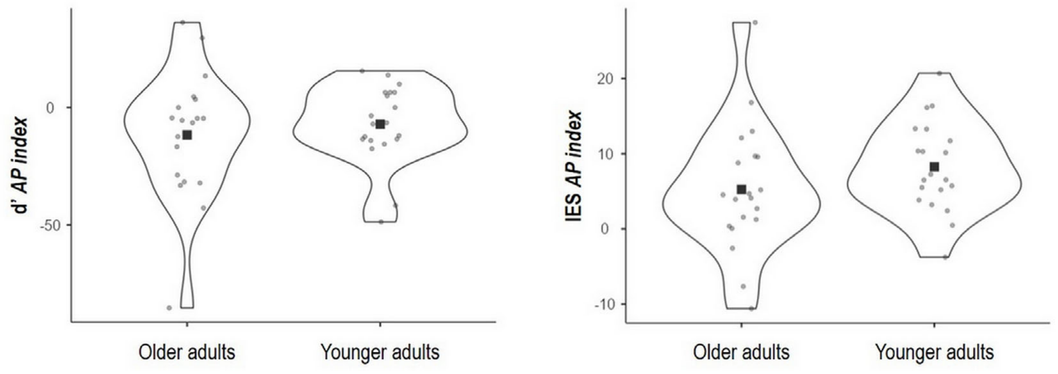

FIGURE 2 The figure illustrates the distribution of the *action prediction (AP) indexes* of performance, calculated on the sensitivity (d', left) and Inverse Efficiency Scores (IES, right) data. The AP indexes normalize each individual's performance at the action prediction task on the performance obtained at the control task (differences expressed in percentage). The raw data are reported in Table 1. The gray dots indicate individual data and the black squares the group means. In the d', the lower the values the worse the sensitivity in the action prediction compared to the control task; in the IES, the higher the values the worse the performance efficiency in the action prediction compared to the control task. As shown by the formal analyses comparing the indexes and by the ANOVA performed on both the d' and the IES raw data, the age-related decay in performance was not specific to the action prediction task.

older adults was not specific to the action prediction task. As a matter of fact, the two groups did not differ in the direct comparison between the "AP indexes" (see Figure 2) calculated by normalizing the individuals' d' calculated for the action prediction task on those calculated for the control task, as follows:

$$\text{Sensitivity}\,(d')\ \text{action prediction}\,(\text{AP})\ \text{index} = [(x-y)/(x+y)] \times 100,$$

where "x" represents the d' in the action prediction task and "y" represents the d' in the control task. The between-group t test performed on this index was not significant ($t(38) = -0.68$, $p > .5$).

3.1.2 | Inverse Efficiency Scores

The ANOVA showed a significant main effect of the task ($F(1,38) = 19.33$, $p < .001$, $\eta_p^2 = 0.34$), indicating that the IESs were lower in the control than the action prediction task in all participants (action prediction task mean IES = 936.29 ± 303.48 ms; control task mean IES = 816.95 ± 256.54 ms). The results also showed a significant main effect of the group ($F(1,38) = 41.28$, $p < .001$, $\eta_p^2 = 0.52$), indicating that the IESs were lower in younger than in older participants (younger group mean IES = 683.32 ± 122.32 ms; older group mean IES = 1015.94 ± 213.79 ms). The group by task interaction was not significant ($F(1,38) = 0.018$, $p = .893$, $\eta_p^2 < 0.01$), indicating that the reduced efficiency shown by the older participants was not specific to the action prediction task. As a matter of fact, the two groups did not differ in the direct comparison between the "AP indexes" (see Figure 2) calculated by normalizing the individuals' IES calculated for the action prediction task on those calculated for the control task, as follows:

$$\text{IES action prediction}\,(\text{AP})\ \text{index} = [(x-y)/(x+y)] \times 100,$$

where "x" represents the individual IESs in the action prediction task and "y" represents the individual IESs in the control task. The between-group t test performed on this index was not significant ($t(38) = -1.30$, $p > .2$).

The analysis of accuracy and RTs is reported in the Supporting Information.

3.2 | fMRI results

3.2.1 | Simple effect of "action prediction > control task" in younger participants

As expected, the results showed that the younger participants recruited a wide network during the action prediction as compared to the control task, including most of the brain regions that are considered to be part of the AON (Grafton, 2009). These regions include bilaterally the superior and inferior parietal lobuli and ventral and dorsal premotor cortices, and the left inferior frontal gyrus and posterior medial frontal cortex (rostral to pre-SMA); in addition, the results showed significant brain activations bilaterally in the lateral occipito-temporal cortex (LOTc) (see Supplementary Table S1 and Figure 3(b)). The simple effect in the opposite direction ("control > action prediction task") showed no significant effect, indicating that no area was more active in the control as compared to the action prediction task in the younger participants.

3.2.2 | Simple effect of "action prediction > control task" in older participants

The results showed that the only brain regions that survived the FWER-correction in older participants comprised two clusters in the

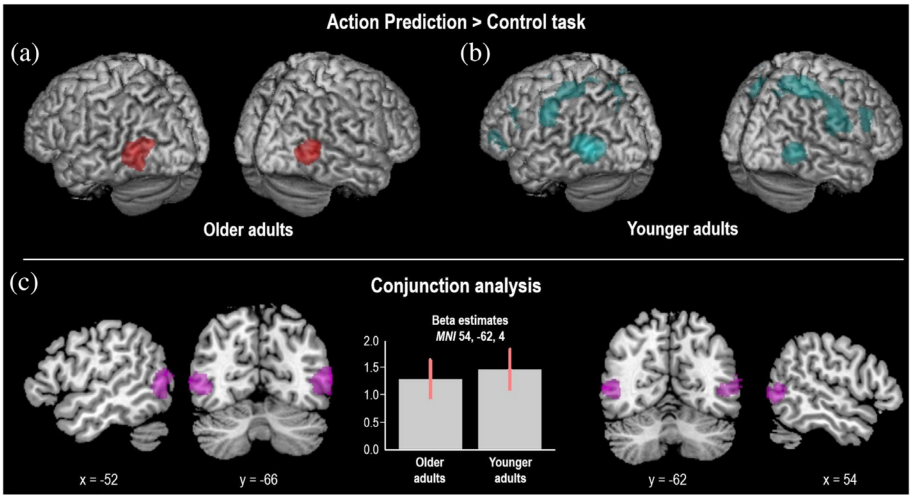

FIGURE 3 The figure illustrates the simple effect of the contrast "action prediction > control task" (a) in the older participants (red), and (b) in the younger participants (cyan). A formal conjunction analysis (c, violet) revealed that the lateral occipito-temporal cortices were commonly recruited by the older and the younger participants. This is also illustrated by the histograms plotting the contrast estimates (beta values, the error bars in the plot indicate the 90% confidence intervals) at the local maxima of the right occipito-temporal cluster (*MNI* 54, −62, 4). All the data are reported by applying the same statistical threshold reported in the tables and discussed in the text ($p_{\text{uncorr}} < .001$ at the voxel level and $p_{\text{FWER-corr}} < .05$ at the cluster level).

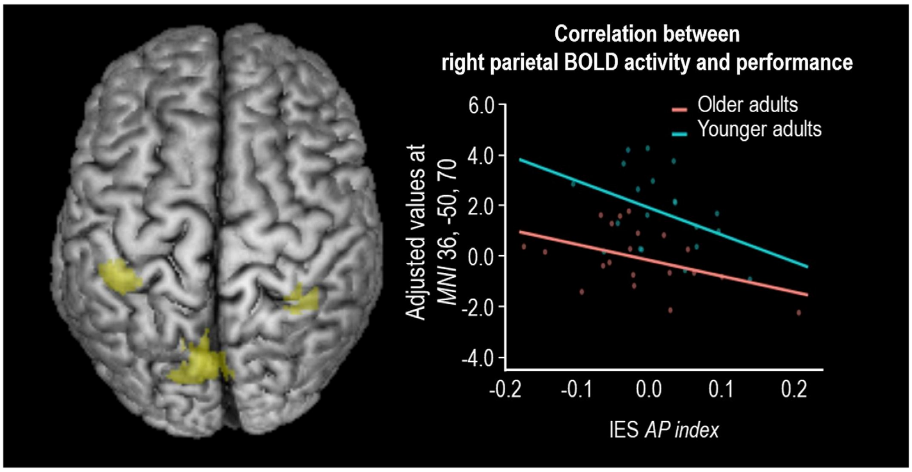

FIGURE 4 The figure (left, yellow) illustrates the hypo-activation shown by the older as compared to the younger participants during the action prediction (as compared to the control) task. The data are reported by applying the same statistical threshold as that reported in the tables and discussed in the text ($p_{\text{uncorr}} < .001$ at the voxel level and $p_{\text{FWER-corr}} < .05$ at the cluster level). The graph on the right plots the parametric association between the brain activations in the action prediction (as compared to the control) task in the right superior parietal lobule (individual adjusted values in the MNI coordinate 36, −50, 70, "y" values in the general linear model [GLM]) and the performance achieved by the participants at the task as measured by the Inverse Efficiency Scores (IES) *action prediction (AP) index*. The red dots indicate the older participants' data and the cyan dots the younger participants' ones.

LOTc bilaterally, including the posterior part of the middle temporal (MT) gyrus (BA 37) and the anterior part of the middle occipital gyrus (BA 19) (see Supplementary Table S2 and Figure 3(a)). The simple effect in the opposite direction ("control > action prediction task") showed no significant effect, indicating that no area was more active in the control as compared to the action prediction task in the older participants.

3.2.3 | Conjunction analysis, "action prediction > control task" in younger ∩ older participants

The conjunction analysis revealed that two clusters in the left and right LOTc were commonly recruited by younger and older participants. These clusters overlapped with the two described above for the simple effect of "action prediction > control task" in both the younger and the older participants (see Table 2(a) and Figure 3(c)).

3.2.4 | Group comparisons measuring age-related differences in the contrast "action prediction > control task"

The results indicated that the older participants hypo-activated, as compared to younger participants, three parietal brain regions, including the precuneus and the superior parietal lobuli bilaterally (see Figure 4 and Table 2(b)). Supplementary Table S3 also reports between-group differences in beta weights extracted from all the clusters showing a significant effect of "action prediction > control task" in younger participants: these comparisons show that other regions within the AON (including dorsal and ventral premotor cortices) were less active in the older as compared to the younger participants, although, as said, the results of the voxel-by-voxel group comparison survived the FWER correction only in the three parietal clusters reported above (Table 2(b)). The contrast in the opposite direction, exploring hyper-activations in the older as compared to the younger participants, showed no significant effect.

3.2.5 | Correlation between brain activations and the behavioral performance

To test the relationship between the individuals' performance at the action prediction task and the BOLD response in the brain regions showing age-related changes, we proceeded as follows. First, we extracted the adjusted y-values (indexing the BOLD effect in each individual) from the local maxima of the three clusters showing a significant effect of age (hypo-activations in the older as compared to the younger participants). The three peaks were located in the precuneus (MNI -6, -74, 56), in the left postcentral gyrus (MNI -44, -36, 6), and in the right superior parietal cortex (36, -50, 70). We then applied a partial correlation aimed to test the parametric association between these brain activations and the behavioral performance as indexed by the IES *AP index* (a measure that summarizes the individual performance at the task). The partial correlation was performed on the whole sample but controlled for the effect of group, to ensure that the parametric association could not be accounted for by group differences in brain activations. The results showed a significant correlation in the right superior parietal cortex ($r = -.41$, $p_{\text{corr}} = .03$). This indicates that, in each group, the higher the activation of the right superior parietal cortex, the better the performance at the action prediction (as compared to the control) task (see Figure 4).

4 | DISCUSSION

The ability to understand others by anticipating the unfolding of their movements has a social valence: it is foundational to motor interaction performance as it enables the prospective preparation of an adaptive response (Bekkering et al., 2009; Candidi et al., 2015; Knoblich & Jordan, 2003; Pecenka & Keller, 2011; Sacheli et al., 2018a, 2018b). Despite the importance of these motor-cognitive abilities in everyday social life, age-related changes in this domain are mostly unexplored. The present study aimed to fill in this gap and evaluated how action prediction is implemented in the aging brain by investigating the case of overlearned movements, like grasping or pointing to an object. We tested whether healthy aging affects the neural resources recruited to anticipate the conclusion of actions during the observation of implied motion pictures: this type of visual stimuli minimizes the complexity of the sensory input and the impact of contextual information while yet evoking (at least in the healthy young participants, see Avenanti et al., 2013; Urgesi et al., 2006, 2010) sensorimotor simulation in the AON (Grafton, 2009).

In line with the evidence for a decline in sensorimotor and cognitive processing in the aging brain (Ren et al., 2013; Seidler et al., 2010), one might expect the older participants to show a specific decay in performance during the action prediction task, which might be paralleled by a reduced involvement of visuo-motor brain regions included in the AON. This pattern of results would support the *reduced embodiment in aging* hypothesis (Costello & Bloesch, 2017; Kuehn et al., 2018). However, in sharp contrast with such a hypothesis, previous studies (Di Tella et al., 2021; Farina et al., 2017; Nedelko et al., 2010) showed that visuo-motor processes sustained by the AON functioning might be particularly resistant to neurophysiological decay in healthy aging, thus suggesting that the AON functioning might show no age-related changes during action prediction as well. We thus designed our study to compare these alternative hypothetical scenarios and reveal how action prediction is implemented in healthy aging. We did so by applying unconstrained neurofunctional analyses at the whole-brain level. The correction for multiple comparisons ensured the robustness of our results.

The behavioral performance of older participants was characterized by a reduced sensitivity and efficiency, which was yet not specific to the action prediction task. Indeed, all the analyses on the behavioral indexes indicated an equal decay in performance in the color discrimination (control) task. This was confirmed by the absence of a significant group difference in the action prediction indexes, that is, the indexes that normalize each individual's performance at the action prediction task on the performance at the control task. Thus, the behavioral results indicate a general age-related performance decay that is yet not specific to the ability to anticipate the conclusion of simple gestures (grasping or pointing actions) but generalizes to a perceptual, nonpredictive, control task.

Nevertheless, the neurofunctional results demonstrated age-related differences specific to action prediction. Indeed, in the contrast "action prediction > control task," the younger participants showed massive recruitment of the whole AON, comprising fronto-temporoparietal regions in both hemispheres, while the older participants mainly recruited the LOTc bilaterally, a brain region including the motion-selective human MT complex (Watson et al., 1993) and the "extrastriate body area" (Downing et al., 2001), as well as other areas involved in processing action-related stimuli (Lingnau & Downing, 2015). Importantly, as a group, the older participants revealed significant hypoactivation in posterior parietal regions that proved to be crucial in the task, as their activation was associated with the level of performance efficiency in both groups. These results have implications for the study of both motor control and social interaction, as discussed below.

4.1 | Action prediction and the action observation network

In line with what was expected based on the previous literature (Avenanti et al., 2013; Urgesi et al., 2006, 2010), the younger participants predicted the conclusion of observed actions by recruiting fronto-temporoparietal brain regions included in the AON. Indeed, the simple effect of "action prediction > control task" in this group showed robust bilateral recruitment of both dorsal and ventral premotor cortices (BA 6 and 44), posterior parietal areas (including BA 7 and 40), and LOTcs (BA 37), as well as activations in the left inferior frontal gyrus and posterior medial frontal cortex. Within these regions, the brain activations in the right parietal cluster were also associated with behavioral performance. Overall, this pattern of results constitutes the *proof of concept* that our action prediction task evokes functionally relevant brain activity in the AON.

It has been widely suggested that the recruitment of the AON depends on the involvement of feed-forward (or generative) internal models (Kilner, 2011). These models allow anticipatory error monitoring during action execution as well as inferences about the conclusion or goal of others' actions during observation (Wolpert et al., 2003). Hypoactivation of the AON during action observation has often been reported when the observer is not able to perform a specific movement, possibly because this, in turn, lowers the accuracy of internal models, thus making them less readily available when interpreting others' actions. This has been shown by studies on children (VanElk et al., 2008) and by research comparing experts (e.g., dancers, musicians, and athletes) with naïve participants (Aglioti et al., 2008; Calvo-Merino et al., 2005, 2006; Candidi et al., 2014; Tomeo et al., 2013). The latter studies show that naïves may achieve performance levels comparable to those of experts during action discrimination/prediction tasks if visual training is allowed, yet without recruiting the motor system to solve the task (Candidi et al., 2014; Mulligan et al., 2016; Urgesi et al., 2012). This result indicates that there might be at least two neurocognitive strategies to approach such tasks, a motorically and a visually based one. Interestingly, participants who performed motor training find it difficult to switch to a nonmotor strategy even when it would be beneficial (as when the motor strategies lead to interference because of a concurrent incongruent motor task, Mulligan et al., 2016). Thus, when possible, the cognitive system tends to recruit motor processes during action observation but yet resolves to visual ones when motor representations are less accessible.

Considering that the present study regarded overlearned actions like grasping and pointing, it seems unreasonable to state that motor representations of such actions might not be as available in our older participants, as they are highly familiar to any individual. Also, our task did not require monitoring the temporal features of the observed movement, thus ruling out that possible slowdowns in movement execution might have modulated the performance of the older participants (see Macerollo et al., 2015). However, widespread action-planning difficulties paralleled by an age-related neurophysiological decline in fronto-parietal areas are well-reported in early healthy aging (Mattay et al., 2002; Ren et al., 2013; Seidler et al., 2010). As we have also shown, this decline impacts on the execution of elementary movements like finger-tapping (Zapparoli et al., 2013) or ankle dorsiflexion (Sacheli et al., 2020), which become more cognitively demanding for older adults. Finally, aging is associated with dedifferentiation in both visual (Park et al., 2004) and motor representations (Carp et al., 2011) that become less vivid and specific. This dedifferentiation process could be conceptualized as a lowering in the accuracy and reliability of internal models with aging: it might have made it more difficult (or inefficient) for older observers to associate the visual stimulus to an appropriate motor representation. This might have led the aging brain to base the perceptual judgment on alternative processing strategies that do not recruit the motor system.

4.2 | Motor cognition and compensatory mechanisms in healthy aging

The first studies on neurofunctional changes across the adult lifespan in several cognitive domains (e.g., working memory, episodic memory retrieval, perception, and inhibitory control) have focused on the hyperactivation of prefrontal regions in older subjects (PASA pattern, Davis et al., 2008). However, it has been shown that compensatory hyperactivation of brain regions in the elderly may also involve task-specific neural circuits outside the frontal lobe (Berlingeri, Bottini, et al., 2010). Concerning motor cognition, visual rather than motor strategies seem to guide the older adults' performance during motor imagery tasks of different complexity (Zapparoli et al., 2013, 2016). Task-specificity in compensatory processes is more in line with the suggestion that cognitive aging is a life-long adaptive process, leading the brain to continuously reorganize to face environmental and physiological challenges (Park & Reuter-Lorenz, 2009), while the lack of reorganization might be what characterizes pathological aging (Berlingeri, Sacheli, et al., 2010). In short, the healthy human brain would unceasingly reshape neural circuits to allow for the maintenance of cognitive performance.

In the present study, we found no evidence of a specific performance deficit in action prediction (compared to the color discrimination control task) nor a specific "compensatory" hyperactivation of brain regions in the older compared to the younger participants. The older adults recruited the same occipito-temporal brain regions recruited by the younger ones. However, they then showed no sign of involvement of fronto-parietal areas, as if the higher-level visual information processing occurring in posterior brain regions was not fed to the visuo-motor nodes of the AON.

In line with the two-streams model of action understanding (Kilner, 2011), the interpretation of others' actions depends on the bidirectional flow of information between visuo-motor fronto-parietal regions coding actions' goals/intentions and higher-order visual regions in the ventral stream (including the LOTc and the posterior part of the superior temporal sulcus) coding the visual features of biological motion and kinematics. Recent evidence of the possibility to decode from LOTc activations also "abstract" features of action representations (like transitivity and sociality, Wurm et al., 2016, 2017) suggests that this region might also be involved in a more abstract (semantic) form of action categorization (Lingnau & Downing, 2015). In our younger participants, the action prediction task concomitantly activated both these regions involved in a more visually guided semantic categorization and those responsible for a more motorically-based fronto-parietal coding, in line with the two-streams model (Kilner, 2011). On the contrary, evidence of recruitment of the LOTc not coupled with fronto-parietal activations in older participants is in line with the hypothesis of a *reduced embodiment* characterizing the aging brain (Costello & Bloesch, 2017; Kuehn et al., 2018) and suggest that, in line with previous evidence in the domain of motor imagery (Zapparoli et al., 2013, 2016), the older participants might have mainly based their performance on visually based rather than motorically based processes. Notably, the age-related hypoactivation included a right parietal cluster whose activity was associated with task performance in both groups. The lack of a specific performance deficit accompanying this reduced activation might be justified by the "young" age of our older participants: it might well be that a retest performed at later stages of the aging processes would reveal the behavioral consequences of such a reduced embodiment, as we showed for other more complex visuo-motor tasks (Zapparoli et al., 2019).

Interestingly, a stronger reliance on visual processing with aging is also present during the execution of reaching and grasping movements. For instance, both Coats and Wann (2011) and Runnarong et al. (2019) demonstrated that movement execution deteriorates when visual feedback is prevented (by occlusion), determining longer adjustment time (Coats & Wann, 2011), longer movement time, and delayed time to maximum velocity (Runnarong et al., 2019) in older but not younger participants. Our results show that the ability to decipher the kinematics of similar hand gestures is also possibly reliant on a visually based coding, leading to reduced recruitment of neurofunctional resources that the literature classically associates with embodied simulation in the AON (Grafton, 2009).

4.3 | Conclusions and implications for social interaction

The findings of the present study suggest that healthy aging is associated with the tendency to under-recruit visuo-motor "mirror" mechanisms (Rizzolatti & Sinigaglia, 2016) in the AON when the individuals have to predict the conclusion of simple gestures in the absence of contextual information. This is paralleled by stable recruitment of higher-level visual areas (the LOTc) that yet seem not to feed information to the fronto-parietal ones.

We reached these conclusions with an experimental paradigm using well-controlled implied-motion postures images, where the hand posture was the only detail to be discriminated. To control for perceptual differences, the target object was kept constant throughout the task: it was a wooden cube with minimal visual features. Of course, this choice makes the stimuli less familiar and associable with real-life situations. They yet ensure that our results were not due to possible confounds linked to image complexity and/or individuals' familiarity with the stimuli. Unlike previous studies in younger participants (see, for instance, Avenanti et al., 2018) that used the prediction of the conclusion of nonhuman movements as a control task, we adopted a color discrimination task to control for the impact of generalized slowdowns in response speed. The lack of a "predictive" control task might yet be a limitation of the study that might be addressed by future research.

Importantly, evidence for reduced recruitment of the AON during action prediction does not necessarily imply that older adults do not recruit the AON when passively observing others. Fronto-parietal activations have been shown during the passive observation of grasping actions in older subjects (Farina et al., 2017; Nedelko et al., 2010). However, these strategies might become less efficient with aging and thus of little use to quickly interpret others' gestures, as required during social exchanges. The anecdotal, real-life report of older adults' minor readiness in responding to conspecifics may depend on a minor efficiency of the motor system in the on-line reading of others' movements. It has been suggested that mirror mechanisms might not be fully established at birth and rather refine (and develop "predictive" features) with time (Natale et al., 2014; Turati et al., 2013), thanks to the maturation of the motor system and repeated experience of action execution and observation (Keysers & Gazzola, 2014). As suggested by recent behavioral studies (Wermelinger et al., 2019), the impoverishing of motor representations in aging might generate an opposite developmental effect. Based on the present study results, future research might address how age-related changes in motor cognition impact the social domain by altering the cognitive strategies applied by healthy older adults during face-to-face interactions. Motor interactions entail a flexible adaptation of "mirror" mechanisms depending on the social contexts (Era et al., 2018; Hadley et al., 2015; Kourtis et al., 2010; Sacheli et al., 2015; Sacheli et al., 2018a, 2018b; Sacheli et al., 2019; Sacheli et al., 2022): whether this flexibility is maintained in the elderly will be the focus of future research.

ACKNOWLEDGMENTS

The study was funded by the Italian Ministry of Health (Ricerca Corrente: protocol L3025, project title "Basi neurali del controllo motorio: pianificazione ed esecuzione motoria nel contesto dell'azione individuale e condivisa"; PI: EP) and by the Milan Center for Neuroscience (NeuroMi). The study was supported by a nationally funded grant from the MIUR (Progetti di Ricerca di Interesse Nazionale, PRIN 2017; project title "The cognitive neuroscience of interpersonal coordination and cooperation: a motor approach in humans and nonhuman primates"; PI: EP; grant n. 2017-NAZ-0435, CUP H45J170006300069).

CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT

Behavioral data are uploaded as Supporting Information (APPENDIX S1). The neurofunctional data can be retrieved from: osf.io/374tj.

ORCID

Lucia Maria Sacheli https://orcid.org/0000-0003-2608-708X

REFERENCES

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, *11*(9), 1109–1116. https://doi.org/10.1038/nn.2182

Appollonio, I., Leone, M., Isella, V., Piamarta, F., Consoli, T., Villa, M. L., Forapani, E., Russo, A., & Nichelli, P. (2005). The frontal assessment battery (FAB): Normative values in an Italian population sample. *Neurological Sciences*, *26*(2), 108–116.

Avenanti, A., Annella, L., Candidi, M., Urgesi, C., & Aglioti, S. M. (2013). Compensatory plasticity in the action observation network: Virtual lesions of STS enhance anticipatory simulation of seen actions. *Cerebral Cortex*, *23*(3), 570–580. https://doi.org/10.1093/cercor/bhs040

Avenanti, A., Paracampo, R., Annella, L., Tidoni, E., & Aglioti, S. M. (2018). Boosting and decreasing action prediction abilities through excitatory and inhibitory TDCS of inferior frontal cortex. *Cerebral Cortex*, *28*(4), 1282–1296. https://doi.org/10.1093/cercor/bhx041

Basso, A., Capitani, E., & Laiacona, M. (1987). Raven's coloured progressive matrices: Normative values on 305 adult normal controls. *Functional Neurology*, *2*(2), 189–194.

Bekkering, H., De Bruijn, E. R. A., Cuijpers, R. H., Newman-Norlund, R., Van Schie, H. T., & Meulenbroek, R. (2009). Joint action: Neurocognitive mechanisms supporting human interaction. *Topics in Cognitive Science*, *1*(2), 340–352. https://doi.org/10.1111/j.1756-8765.2009.01023.x

Berlingeri, M., Bottini, G., Danelli, L., Ferri, F., Traficante, D., Sacheli, L., Colombo, N., Sberna, M., Sterzi, R., Scialfa, G., & Paulesu, E. (2010). With time on our side? Task-dependent compensatory processes in graceful aging. *Experimental Brain Research*, *205*(3), 307–324. https://doi.org/10.1007/s00221-010-2363-7

Berlingeri, M., Sacheli, L., Danelli, L., Ferri, F., Traficante, D., Basilico, S., Sberna, M., Sterzi, R., Bottini, G., & Paulesu, E. (2010). Neurofunctional and neuromorphological evidence of the lack of compensation in pathological aging. *Behavioural Neurology*, *23*(4), 185–187. https://doi.org/10.3233/BEN-2010-0290

Binkofski, F., & Buccino, G. (2018). The role of the parietal cortex in sensorimotor transformations and action coding. In *Handbook of clinical neurology* (Vol. 151, 1st ed.). Elsevier B.V. https://doi.org/10.1016/B978-0-444-63622-5.00024-3

Blakemore, S. J., & Sirigu, A. (2003). Action prediction in the cerebellum and in the parietal lobe. *Experimental Brain Research*, *153*(2), 239–245. https://doi.org/10.1007/s00221-003-1597-z

Bruyer, R., & Brysbaert, M. (2011). Combining speed and accuracy in cognitive psychology: Is the inverse efficiency score (IES) a better dependent variable than the mean reaction time (RT) and the percentage of errors (PE)? *Psychologica Belgica*, *51*(1), 5–13. https://doi.org/10.5334/pb-51-1-5

Buccino, G. (2014). Action observation treatment: A novel tool in neurorehabilitation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1644), 20130185. https://doi.org/10.1098/rstb.2013.0185

Buckles, V. D. (1993). Age-related slowing. In *Sensorimotor impairment in the elderly* (pp. 73–87). Springer.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An FMRI study with expert dancers. *Cerebral Cortex*, *15*(8), 1243–1249. https://doi.org/10.1093/cercor/bhi007

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, *16*(19), 1905–1910. https://doi.org/10.1016/j.cub.2006.07.065

Candidi, M., Sacheli, L. M., & Aglioti, S. M. (2015). From muscles synergies and individual goals to interpersonal synergies and shared goals: Mirror neurons and interpersonal action hierarchies. Comment on 'Grasping synergies: A motor-control approach to the mirror neuron mechanism' by D'Ausilio et al. *Physics of Life Reviews*, *12*, 126–128. https://doi.org/10.1016/j.plrev.2015.01.023

Candidi, M., Sacheli, L. M., Mega, I., & Aglioti, S. M. (2014). Somatotopic mapping of piano fingering errors in sensorimotor experts: TMS studies in pianists and visually trained musically Naïves. *Cerebral Cortex*, *24*(2), 435–443. https://doi.org/10.1093/cercor/bhs325

Carp, J., Park, J., Hebrank, A., Park, D. C., & Polk, T. A. (2011). Age-related neural dedifferentiation in the motor system. *PLoS One*, *6*(12), 1–6. https://doi.org/10.1371/journal.pone.0029411

Chong, T. T. J., Cunnington, R., Williams, M. A., Kanwisher, N., & Mattingley, J. B. (2008). FMRI adaptation reveals mirror neurons in human inferior parietal cortex. *Current Biology*, *18*(20), 1576–1580. https://doi.org/10.1016/j.cub.2008.08.068

Coats, R. O., & Wann, J. P. (2011). The reliance on visual feedback control by older adults is highlighted in tasks requiring precise endpoint placement and precision grip. *Experimental Brain Research*, *214*(1), 139–150. https://doi.org/10.1007/s00221-011-2813-x

Costello, M. C., & Bloesch, E. K. (2017). Are older adults less embodied? A review of age effects through the lens of embodied cognition. *Frontiers in Psychology*, *8*, 267. https://doi.org/10.3389/fpsyg.2017.00267

Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M., & Cabeza, R. (2008). Qué PASA? The posterior-anterior shift in aging. *Cerebral Cortex*, *18*(5), 1201–1209. https://doi.org/10.1021/nn2045246.Multifunctional

Di Tella, S., Blasi, V., Cabinio, M., Bergsland, N., Buccino, G., & Baglio, F. (2021). How do we motorically resonate in aging? A compensatory role of prefrontal cortex. *Frontiers in Aging Neuroscience*, *13*, 694676. https://doi.org/10.3389/fnagi.2021.694676

Diersch, N., Cross, E. S., Stadler, W., Schütz-Bosbach, S., & Rieger, M. (2012). Representing others' actions: The role of expertise in the aging mind. *Psychological Research*, *76*(4), 525–541. https://doi.org/10.1007/s00426-011-0404-x

Diersch, N., Jones, A. L., & Cross, E. S. (2016). The timing and precision of action prediction in the aging brain. *Human Brain Mapping*, *37*(1), 54–66. https://doi.org/10.1002/hbm.23012

Diersch, N., Mueller, K., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (2013). Action prediction in younger versus older adults: Neural correlates of motor familiarity. *PLoS One*, *8*(5), e64195. https://doi.org/10.1371/journal.pone.0064195

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*(5539), 2470–2473. https://doi.org/10.1126/science.1063414

Era, V., Candidi, M., Gandolfo, M., Sacheli, L. M., & Aglioti, S. M. (2018). Inhibition of left anterior intraparietal sulcus shows that mutual adjustment marks dyadic joint-actions in humans. *Social Cognitive and Affective Neuroscience*, *13*(5), 492–500. https://doi.org/10.1093/scan/nsy022

Farina, E., Baglio, F., Pomati, S., D'Amico, A., Campini, I. C., Tella, S., Di Belloni, G., & Pozzo, T. (2017). The mirror neurons network in aging, mild cognitive impairment, and Alzheimer disease: A functional MRI study. *Frontiers in Aging Neuroscience*, *9*, 371.

Flandin, G., & Friston, K. J. (2019). Analysis of family-wise error rates in statistical parametric mapping using random field theory. *Human Brain Mapping*, *40*(7), 2052–2054. https://doi.org/10.1002/hbm.23839

Friston, K., Mattout, J., & Kilner, J. (2011). Action understanding and active inference. *Biological Cybernetics*, *104*(1–2), 137–160. https://doi.org/10.1007/s00422-011-0424-z

Grafton, S. T. (2009). Embodied cognition and the simulation of action to understand others. *Annals of the New York Academy of Sciences*, *1156*, 97–117. https://doi.org/10.1111/j.1749-6632.2009.04425.x

Hadley, L. V., Novembre, G., Keller, P. E., & Pickering, M. J. (2015). Causal role of motor simulation in turn-taking behavior. *Journal of Neuroscience*, *35*(50), 16516–16520. https://doi.org/10.1523/JNEUROSCI.1850-15.2015

Hardwick, R. M., Caspers, S., Eickhoff, S. B., & Swinnen, S. P. (2018). Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. *Neuroscience and Biobehavioral Reviews*, *94*, 31–44. https://doi.org/10.1016/j.neubiorev.2018.08.003

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*(5), 849–878. https://doi.org/10.1017/S0140525X01000103

Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, *14*(1 II), 103–109. https://doi.org/10.1006/nimg.2001.0832

Keller, P. E., Novembre, G., & Hove, M. J. (2014). Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal coordination. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1658), 20130394. https://doi.org/10.1098/rstb.2013.0394

Keysers, C., & Gazzola, V. (2014). Hebbian learning and predictive mirror neurons for actions, sensations and emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1644), 20130175. https://doi.org/10.1098/rstb.2013.0175

Kilner, J. M. (2011). More than one pathway to action understanding. *Trends in Cognitive Sciences*, *15*(8), 352–357. https://doi.org/10.1016/j.tics.2011.06.005

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). The mirror-neuron system: A Bayesian perspective. *Neuroreport*, *18*(6), 619–623. https://doi.org/10.1097/WNR.0b013e3281139ed0

Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience*, *29*(32), 10153–10159. https://doi.org/10.1523/JNEUROSCI.2668-09.2009

Knoblich, G., & Jordan, J. S. (2003). Action coordination in groups and individuals: Learning anticipatory control. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *29*(5), 1006–1016. https://doi.org/10.1037/0278-7393.29.5.1006

Kourtis, D., Sebanz, N., & Knoblich, G. (2010). Favouritism in the motor system: Social interaction modulates action simulation. *Biology Letters*, *6*(6), 758–761. https://doi.org/10.1098/rsbl.2010.0478

Kuehn, E., Perez-Lopez, M. B., Diersch, N., Döhler, J., Wolbers, T., & Riemer, M. (2018). Embodiment in the aging mind. *Neuroscience and Biobehavioral Reviews*, *86*, 207–225. https://doi.org/10.1016/j.neubiorev.2017.11.016

Lingnau, A., & Downing, P. E. (2015). The lateral occipitotemporal cortex in action. *Trends in Cognitive Sciences*, *19*(5), 268–277. https://doi.org/10.1016/j.tics.2015.03.006

Macerollo, A., Bose, S., Ricciardi, L., Edwards, M. J., & Kilner, J. M. (2015). Linking differences in action perception with differences in action execution. *Social Cognitive and Affective Neuroscience*, *10*(8), 1121–1127.

Makris, S., & Urgesi, C. (2015). Neural underpinnings of superior action prediction abilities in soccer players. *Social Cognitive and Affective Neuroscience*, *10*(3), 342–351. https://doi.org/10.1093/scan/nsu052

Mattay, V. S., Fera, F., Tessitore, A., Hariri, A. R., Das, S., Callicott, J. H., & Weinberger, D. R. (2002). Neurophysiological correlates of age-related changes in human motor function. *Neurology*, *58*(4), 630–635. https://doi.org/10.1212/WNL.58.4.630

Measso, G., Cavarzeran, F., Zappalà, G., Lebowitz, B. D., Crook, T. H., Pirozzolo, F. J., Amaducci, L. A., Massari, D., & Grigoletto, F. (1993). The mini-mental state examination: Normative study of an Italian random sample. *Developmental Neuropsychology*, *9*(2), 77–85.

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology*, *20*(8), 750–756. https://doi.org/10.1016/j.cub.2010.02.045

Mulligan, D., Lohse, K. R., & Hodges, N. J. (2016). Evidence for dual mechanisms of action prediction dependent on acquired visual-motor experiences. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(10), 1615–1626. https://doi.org/10.1037/xhp0000241

Natale, E., Senna, I., Bolognini, N., Quadrelli, E., Addabbo, M., Macchi Cassia, V., & Turati, C. (2014). Predicting others' intention involves motor resonance: EMG evidence from 6- and 9-month-old infants. *Developmental Cognitive Neuroscience*, *7*, 23–29.

Nebes, R. D. (1978). Vocal versus manual response as a determinant of age difference in simple reaction time. *Journal of Gerontology*, *33*(6), 884–889.

Nedelko, V., Hassa, T., Hamzei, F., Weiller, C., Binkofski, F., Schoenfeld, M. A., Tüscher, O., & Dettmers, C. (2010). Age-independent activation in areas of the mirror neuron system during action observation and action imagery. A fMRI study. *Restorative Neurology and Neuroscience*, *28*(6), 737–747. https://doi.org/10.3233/RNN-2010-0542

Novembre, G., & Keller, P. E. (2014). A conceptual review on action-perception coupling in the musicians' brain: What is it good for? *Frontiers in Human Neuroscience*, *8*, 603. https://doi.org/10.3389/fnhum.2014.00603

Novembre, G., Ticini, L. F., Schütz-Bosbach, S., & Keller, P. E. (2012). Distinguishing self and other in joint action. Evidence from a musical paradigm. *Cerebral Cortex*, *22*(12), 2894–2903. https://doi.org/10.1093/cercor/bhr364

Novembre, G., Ticini, L. F., Schütz-Bosbach, S., & Keller, P. E. (2014). Motor simulation and the coordination of self and other in real-time joint action. *Social Cognitive and Affective Neuroscience*, *9*(8), 1062–1068. https://doi.org/10.1093/scan/nst086

Orsini, A., Grossi, D., Capitani, E., Laiacona, M., Papagno, C., & Vallar, G. (1987). Verbal and spatial immediate memory span: Normative data from 1355 adults and 1112 children. *The Italian Journal of Neurological Sciences*, *8*(6), 539–548. https://doi.org/10.1007/BF02333660

Park, D. C., Polk, T. A., Park, R., Minear, M., Savage, A., & Smith, M. R. (2004). Aging reduces neural specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(35), 13091–13095. https://doi.org/10.1073/pnas.0405148101

Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*, *60*, 173–196. https://doi.org/10.1146/annurev.psych.59.103006.093656

Pecenka, N., & Keller, P. E. (2011). The role of temporal prediction abilities in interpersonal sensorimotor synchronization. *Experimental Brain Research*, *211*(3–4), 505–515. https://doi.org/10.1007/s00221-011-2616-0

Personnier, P., Paizis, C., Ballay, Y., & Papaxanthis, C. (2008). Mentally represented motor actions in normal aging. II. The influence of the gravito-inertial context on the duration of overt and covert arm movements. *Behavioural Brain Research*, *186*(2), 273–283. https://doi.org/10.1016/j.bbr.2007.08.018

Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, *9*(2), 129–154. https://doi.org/10.1080/713752551

Ren, J., Wu, Y. D., Chan, J. S. Y., & Yan, J. H. (2013). Cognitive aging affects motor performance and learning. *Geriatrics and Gerontology International*, *13*(1), 19–27. https://doi.org/10.1111/j.1447-0594.2012.00914.x

Rizzolatti, G., & Sinigaglia, C. (2016). The mirror mechanism: A basic principle of brain function. *Nature Reviews Neuroscience*, *17*(12), 757–765. https://doi.org/10.1038/nrn.2016.135

Runnarong, N., Tretriluxana, J., Waiyasil, W., Sittisupapong, P., & Tretriluxana, S. (2019). Age-related changes in reach-to-grasp movements with partial visual occlusion. *PLoS One*, *14*(8), 1–15. https://doi.org/10.1371/journal.pone.0221320

Sacheli, L. M., Arcangeli, E., & Paulesu, E. (2018a). Evidence for a dyadic motor plan in joint action. *Scientific Reports*, *8*, 5027. https://doi.org/10.1038/s41598-018-23275-9

Sacheli, L. M., Candidi, M., Era, V., & Aglioti, S. M. (2015). Causative role of left AIPS in coding shared goals during human-avatar complementary joint actions. *Nature Communications*, *6*, 7544. https://doi.org/10.1038/ncomms8544

Sacheli, L. M., Musco, M. A., Zazzera, E., Banfi, G., & Paulesu, E. (2022). How shared goals shape action monitoring. *Cerebral Cortex*, bhac019. Advance online publication. https://doi.org/10.1093/cercor/bhac019

Sacheli, L. M., Tieri, G., Aglioti, S. M., & Candidi, M. (2018b). Transitory inhibition of the left anterior intraparietal sulcus impairs joint actions: A continuous theta-burst stimulation study. *Journal of Cognitive Neuroscience*, *30*(5), 737–751. https://doi.org/10.1162/jocn_a_01227

Sacheli, L. M., Verga, C., Arcangeli, E., Banfi, G., Tettamanti, M., & Paulesu, E. (2019). How task interactivity shapes action observation. *Cerebral Cortex*, *29*(12), 5302–5314. https://doi.org/10.1093/cercor/bhz205

Sacheli, L. M., Zapparoli, L., Bonandrini, R., Preti, M., Pelosi, C., Sconfienza, L. M., Banfi, G., & Paulesu, E. (2020). How aging affects the premotor control of lower limb movements in simulated gait. *Human Brain Mapping*, *41*(7), 1889–1903. https://doi.org/10.1002/hbm.24919

Saimpont, A., Malouin, F., Tousignant, B., & Jackson, P. L. (2013). Motor imagery and aging. *Journal of Motor Behavior*, *45*(1), 21–28. https://doi.org/10.1080/00222895.2012.740098

Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Research Bulletin*, *70*(4–6), 337–346. https://doi.org/10.1016/j.brainresbull.2006.06.008

Seidler, R. D., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., Kwak, Y., & Lipps, D. B. (2010). Motor control and aging: Links to age-related brain structural, functional, and biochemical effects. *Neuroscience and Biobehavioral Reviews*, *34*(5), 721–733. https://doi.org/10.1016/j.neubiorev.2009.10.005

Skoura, X., Papaxanthis, C., Vinter, A., & Pozzo, T. (2005). Mentally represented motor actions in normal aging: I. Age effects on the temporal features of overt and covert execution of actions. *Behavioural Brain Research*, *165*(2), 229–239. https://doi.org/10.1016/j.bbr.2005.07.023

Stadler, W., Ott, D. V. M., Springer, A., Schubotz, R. I., Schütz-Bosbach, S., & Prinz, W. (2012). Repetitive TMS suggests a role of the human dorsal premotor cortex in action prediction. *Frontiers in Human Neuroscience*, *6*-(January), 20. https://doi.org/10.3389/fnhum.2012.00020

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *3*(I), 137–149.

Tomeo, E., Cesari, P., Aglioti, S. M., & Urgesi, C. (2013). Fooling the kickers but not the goalkeepers: Behavioral and neurophysiological correlates of fake action detection in soccer. *Cerebral Cortex*, *23*(11), 2765–2778. https://doi.org/10.1093/cercor/bhs279

Tunik, E., Rice, N. J., Hamilton, A., & Grafton, S. T. (2007). Beyond grasping: Representation of action in human anterior intraparietal sulcus. *NeuroImage*, *36*(Suppl 2), T77–T86.

Turati, C., Natale, E., Bolognini, N., Senna, I., Picozzi, M., Longhi, E., & Cassia, V. M. (2013). The early development of human mirror mechanisms: Evidence from electromyographic recordings at 3 and 6 months. *Developmental Science*, *16*(6), 793–800. https://doi.org/10.1111/desc.12066

Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, *31*(1), 155–165.

Urgesi, C., Maieron, M., Avenanti, A., Tidoni, E., Fabbro, F., & Aglioti, S. M. (2010). Simulating the future of actions in the human corticospinal system. *Cerebral Cortex*, *20*(11), 2511–2521. https://doi.org/10.1093/cercor/bhp292

Urgesi, C., Moro, V., Candidi, M., & Aglioti, S. M. (2006). Mapping implied body actions in the human motor system. *Journal of Neuroscience*, *26*(30), 7942–7949.

Urgesi, C., Savonitto, M. M., Fabbro, F., & Aglioti, S. M. (2012). Long- and short-term plastic modeling of action prediction abilities in volleyball. *Psychological Research*, *76*(4), 542–560. https://doi.org/10.1007/s00426-011-0383-y

VanElk, M., VanSchie, H. T., Hunnius, S., Vesper, C., & Bekkering, H. (2008). You'll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *NeuroImage*, *43*(4), 808–814. https://doi.org/10.1016/j.neuroimage.2008.07.057

Watson, J. D., Myers, R., Frackowiak, R. S., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., Shipp, S., & Zeki, S. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex*, *3*(2), 79–94. https://doi.org/10.1093/cercor/3.2.79

Wermelinger, S., Gampe, A., & Daum, M. M. (2019). The dynamics of the interrelation of perception and action across the life span. *Psychological Research*, *83*(1), 116–131. https://doi.org/10.1007/s00426-018-1058-8

Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *358*(1431), 593–602. https://doi.org/10.1098/rstb.2002.1238

Worsley, K. J., & Friston, K. J. (1995). Analysis of FMRI time-series revisited—Again. *NeuroImage*, *2*(3), 173–181.

Wurm, M. F., Ariani, G., Greenlee, M. W., & Lingnau, A. (2016). Decoding concrete and abstract action representations during explicit and implicit conceptual processing. *Cerebral Cortex*, *26*(8), 3390–3401. https://doi.org/10.1093/cercor/bhv169

Wurm, M. F., Caramazza, A., & Lingnau, A. (2017). Action categories in lateral occipitotemporal cortex are organized along sociality and transitivity. *Journal of Neuroscience*, *37*(3), 562–575. https://doi.org/10.1523/JNEUROSCI.1717-16.2016

Zapparoli, L., Gandola, M., Banfi, G., & Paulesu, E. (2019). A breakdown of imagined visuomotor transformations and its neural correlates in young elderly subjects. *Cerebral Cortex*, *29*(4), 1682–1696. https://doi.org/10.1093/cercor/bhy314

Zapparoli, L., Invernizzi, P., Gandola, M., Verardi, M., Berlingeri, M., Sberna, M., De Santis, A., Zerbi, A., Banfi, G., Bottini, G., & Paulesu, E. (2013). Mental images across the adult lifespan: A behavioural and FMRI investigation of motor execution and motor imagery. *Experimental Brain Research*, *224*(4), 519–540.

Zapparoli, L., Saetta, G., De Santis, C., Gandola, M., Zerbi, A., Banfi, G., & Paulesu, E. (2016). When I am (almost) 64: The effect of normal ageing on implicit motor imagery in young elderlies. *Behavioural Brain Research*, *303*, 137–151. https://doi.org/10.1016/j.bbr.2016.01.058

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sacheli, L. M., Verga, C., Zapparoli, L., Seghezzi, S., Tomasetig, G., Banfi, G., & Paulesu, E. (2023). When action prediction grows old: An fMRI study. *Human Brain Mapping*, *44*(2), 373–387. https://doi.org/10.1002/hbm.26049