Vision- and touch-dependent brain correlates of body-related mental processing
Research Report

Vision- and touch-dependent brain correlates of body-related mental processing

Gustavo S.P. Pamplona a,b, Martina Hardmeier a,c, Sofian Younes a, Isabelle Goy a, Eleonora Fornari d,e and Silvio Ionta a, *

a Sensory-Motor Lab (SeMoLa), Department of Ophthalmology-University of Lausanne, Jules Gonin Eye Hospital-Fondation Asile des Aveugles, Lausanne, Switzerland
b Rehabilitation Engineering Laboratory (RELab), Department of Health Sciences and Technology, ETH Zurich, Zurich, Switzerland
c Department of Psychology, University of Fribourg, Fribourg, Switzerland
d CIBM Center for Biomedical Imaging, Lausanne, Switzerland
e Department of Diagnostic and Interventional Radiology, Lausanne University Hospital and University of Lausanne, Lausanne, Switzerland

ABSTRACT

In humans, the nature of sensory input influences body-related mental processing. For instance, behavioral differences (e.g., response time) can be found between mental spatial transformations (e.g., mental rotation) of viewed and touched body parts. It can thus be hypothesized that distinct brain activation patterns are associated with such sensory-dependent body-related mental processing. However, direct evidence that the neural correlates of body-related mental processing can be modulated by the nature of the sensory stimuli is still missing. We thus analyzed event-related functional magnetic resonance imaging (fMRI) data from thirty-one healthy participants performing mental rotation of visually- (images) and haptically-presented (plastic) hands. We also dissociated the neural activity related to rotation or task-related performance using models that either regressed out or included the variance associated with response time. Haptically-mediated mental rotation recruited mostly the sensorimotor brain network. Visually-mediated mental rotation led to parieto-occipital activations. In addition, faster mental rotation was associated with sensorimotor activity, while slower mental rotation was associated with parieto-occipital activations. The fMRI results indicated that changing the type of sensory inputs modulates the neural correlates of body-related mental processing. These findings suggest that distinct sensorimotor brain dynamics can be exploited to execute similar tasks depending on the available sensory input. The present study can contribute to a better evaluation of body-related mental processing in experimental and clinical settings.

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1. Introduction

Imagine a cold winter morning. You are about to go out and want to put on the disarranged gloves that you threw on the table the night before. How do you know which glove goes on which hand? The last decades of cognitive neuroscience research indicated that we would unconsciously perform a mental rotation of the image of each glove in order to check whether it fits the left or the right hand (Parsons, 1987). Mental rotation refers to the well-studied human ability to mentally “move” an object without physically moving it (visual imagery) (Kosslyn et al., 2001). In the case of mental rotation of a body part (e.g., hands), one can also imagine moving one’s own body part to match the target object (motor imagery) (Munzert & Zentgraf, 2009). The difference between visual and motor imagery is supported by recent neuroimaging studies (Berneiser et al., 2018; de Lange et al., 2006; Ionta et al., 2016; Kashuk et al., 2017; Perruchoud et al., 2016; Tomasino & Gremese, 2016; Vingerhoets et al., 2002; Zapparoli et al., 2014) showing that mental rotation of hands can be associated with neural activations in visual and/or sensorimotor brain regions, respectively involved in visual (Tomasino & Gremese, 2016) or motor imagery (Hétu et al., 2013).

However, rather than being invariant, the balance between the visual and motor imagery components of mental rotation of body parts can vary, depending on contextual factors such as the reliability/availability of sensory input (Ionta et al., 2016), eventual implicit identification (Zeugin et al., 2017), and sensorimotor experience (Scandola et al., 2019). Revealing the neural correlates of such a flexible relationship between visual and motor imagery components in mental rotation of body parts is of paramount importance, for instance, in the context of screening tools to establish the status of sensory processing in clinical conditions.

Previous studies attempted to modulate this visuo/motor relationship through manipulating the (visual) stimulus [e.g., comparing hands with full-body pictures (Perruchoud et al., 2016)], instructing to adopt different first- or third-person perspectives (Tomasino & Gremese, 2016), presenting either the dorsum or the palm of the hand (Bässing et al., 2013; Zapparoli et al., 2014), or exposing participants to trainings able to induce visual-to-motor shifts in the imagery strategy (Berneiser et al., 2018). However, manipulating the visual input might implicitly trigger top-down driven visual imagery before the onset of supporting motor imagery (Prather & Sathian, 2002). Conversely, haptic perception (based on the sense of touch) might generate mental images without intervention of visual imagery (Kitada et al., 2010) and lead to bottom-up processing (Kitada et al., 2010; Kitada et al., 2010). Therefore, changing the sensory input (visual vs haptic) for mental rotation of hands could be an efficient way to modulate the relative weighting between visual and motor imagery.

Although similar findings on response time have been reported in the context of both visually- (Chen et al., 2019; Cooper & Shepard, 1975; Ionta et al., 2007; Parsons, 1994; Sekiyama, 1982) and haptically-based mental rotation of hands (Kitada et al., 2010; Rangel et al., 2010), the neural differences between haptically- and visually-mediated mental rotation of hands are not yet fully understood. Since the relative weighting of the type of imagery in mental rotation of hands may result in distinct patterns of brain activity, our null hypothesis is that mental rotation of both visually- and haptically-presented hands triggers the same type of mental imagery, leading to similar patterns of brain activity. The alternative hypothesis is that, compared to mental rotation of visually-presented hands, mental rotation of haptically-presented hands would rely more on motor imagery and therefore would be associated with stronger neural activity in the sensorimotor regions of the brain. Conversely, compared to haptically-presented hands, mental rotation of visually-presented hands would rely more on visual imagery and therefore would be associated with stronger activity in visual regions.

In addition, the type of sensory input stimuli may also modulate the interference of the internally-directed cognition during mental rotation. The activation of the default mode network (DMN) is related to internally-oriented attention (Andrews-Hanna et al., 2014; Fox et al., 2005; Raichle et al., 2001) and considered detrimental for externally-oriented task performance (Mason et al., 2007; Weissman et al., 2006). Therefore, incremental perceptual updating in the haptic stimuli exploration (and therefore high cognitive load (Rangel et al., 2010)) versus the immediate perception of visual stimuli should result in less interference of DMN activity on haptic mental rotation of hands. Thus, we also hypothesize that a greater interference of internally-directed cognition on task performance is observed mainly through activity in the default mode network (DMN) during presentation of visual stimuli.

To test these hypotheses, we performed an fMRI event-related experiment in which 31 individuals performed mental rotation of haptically- and visually-presented hands. The experiment was controlled for the mere exposure to haptic and visual stimuli across conditions, i.e., while participants explored the hand stimulus haptically (visually), they simultaneously observed (haptically explored) a sphere. Furthermore, brain activation was adjusted by the response time measured in a self-paced design. We assessed differences in the dependence of brain activity and its association with performance in mental rotation of hands across sensory input (Modality) and orientations (Rotation), reflecting the relative weighting between motor and visual imagery.

2. Materials and methods

The study protocol was approved by the cantonal ethics committee and the experiment was performed in accordance with the Declaration of Helsinki (2013). All participants provided written consent prior to entering in the study, as well as to a safety questionnaire for the magnetic resonance (MR) exam, and received monetary compensation was provided for the time spent in the experiment. Participants were naïve to the research questions until the end of the experiment. No part of the study procedures was pre-registered prior to the research being conducted. Here we report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. The conditions of our ethics approval do not permit public archiving of raw anonymized magnetic resonance
imaging (MRI) data. In order to guarantee confidentiality, queries by readers seeking access to the data should be submitted to and will be evaluated by the corresponding author(s), access to data may be granted to named individuals in accordance with the study’s procedures governing the reuse of sensitive data, and any potential reuse should be subject to completion of a formal data sharing agreement/contract.

2.1. Participants

Thirty-three healthy, right-handed individuals participated in the study. Data from two participants were not analyzed/recorded due to incidental findings and experienced discomfort in the magnetic resonance (MR) environment, respectively. The remaining thirty-one participants’ age (24.4 ± 2.4 years old; range = 21.5–32.1 years old) was not different between genders (14 women; Wilcoxon test: p = .18). Exclusion criteria at recruitment were: age out of pre-established range (18–40 years old); insufficient verbal abilities in either English or French, necessary to follow the instructions; left-handedness, defined by scores lower than the cut-off of 60 in the Edinburgh Handedness Inventory (Oldfield, 1971) (https://www.brainmapping.org/shared/Edinburgh.php); history of neurological, psychiatric, or cardiovascular disorders; vision impairments (outside of –3 to +3 dioptries, when correction by contact lenses was not possible); no compliance in abstaining from use of alcohol or other drugs during the days of experiment; MR contraindications; hand amputation; claustrophobia; pregnancy or breastfeeding.

2.2. Experimental procedure

Participants performed mental rotation of visually- or haptically-presented hands during fMRI data acquisition. Visually-presented hands consisted of pictures of a human hand (visual stimuli). Haptically-presented hands (haptic stimuli) consisted of three-dimensional hands made of polyvinyl chloride (hard plastic). Participants judged the laterality of each stimulus. Both the visual and haptic stimuli could vary in terms of Rotation (0°, 90°, 180°, 270°), View (palm or dorsum), and Laterality (left or right), totaling 16 possible combinations for each sensory modality (Fig. 1A). For the visual stimuli, the upright Rotation (0°) was defined as fingers pointing upwards. For haptic stimuli the upright Rotation corresponded to the plastic hand placed in the same direction as the participants’ right hand. The upside-down Rotation (180°) was defined as fingers pointing downwards for visual stimuli, and as the plastic hand placed in the opposite direction with respect to the participant’s right hand for haptic stimuli. Considering that mental rotation of hands is faster for stimuli oriented toward than away from the individual’s midsagittal plane (Funk & Brugger, 2008; Ionta et al., 2013; Parsons, 1994), for both the dorsum and palm views, right hands presented at 90° and left hands presented at 270° (according to a clockwise rotation from the upright hand posture) were defined as “lateral rotations” (Lat). Conversely, also for both the dorsum and palm views, right hands presented at 270° and left hands presented at 90° (according to a clockwise rotation from the upright posture) were defined as “medial rotations” (Med).

The mental rotation task is outlined in Fig. 1B. In each trial, participants judged the handedness of a stimulus, rotated in different orientations. In each trial, participants received a hand stimulus in either the visual or the haptic modality. To control for possible differences in mere sensory processing between conditions, in the haptic condition participants explored the hand stimulus haptically and simultaneously observed a wooden sphere on the screen (scaled to the same size ratio of the visual hand stimuli); while in the visual condition participants explored the hand stimulus visually and simultaneously touched a Styrofoam half sphere (Holdstock et al., 2009). This way, every trial contained elements of both haptic and visual processing, but only one of them contained the hand stimulus relevant for the mental rotation task. Participants were neither able to see the haptic stimuli nor their own hands while performing the task. Before the MR acquisition, all participants received instructions about the task, which included responding as fast and as accurately as possible without guessing and to gently and thoroughly stroke either the hand stimuli or the half sphere while keeping the rest of the body still.

The presentation of the stimuli was guided by a customized code, written in MATLAB (The MathWorks, Natick, MA, USA) and Psychtoolbox (http://psychtoolbox.org) and run on a dedicated Windows laptop. Directly before the MR functional acquisition, participants were reminded of the task procedure through written instructions on the screen, which included starting with the forearm raised, supported by the elbow. Then, the fMRI acquisition started with the message “Experiment starting” followed by a small black fixation cross on the center of a white background screen for 12 sec. Next, a 1-sec black down-arrow signaled the participant to lower the right forearm and start either the haptic exploration of the hand stimulus (while viewing a sphere) or the haptic exploration of the half sphere (while viewing the hand stimulus). The participant then responded with the laterality of the hand stimulus (either visual or haptic) by pressing one of the buttons of a response pad, positioned on the left hand. Participants should indicate the laterality of the left- or right-hand stimulus by pressing the left- or right-buttons on the response pad with their left middle or index fingers, respectively. The visual (haptic) stimuli remained on the screen (under the participant’s hand) until the participant’s response or for a maximum of 6 sec. Next, a 1-sec black up-arrow indicated that the right forearm should be raised. Finally, a fixation cross remained on the screen until the down-arrow was presented again in the next trial. The period for the fixation cross was 6 sec – RT + tfix, in which RT is the participant’s response time on the trial and tfix is a randomized period that could last between 3 and 4.5 sec, in steps of .5 sec, to jitter stimulus onset. Intervals for stimulus and fixation cross presentation were defined based on both visuotactile studies (Saito et al., 2003; Tal & Amedi, 2009) and pilot experiments. Each run comprised of 32 trials and each possible combination [2 sensory Modalities (haptic/visual) × 4 Rotations (0°/Med/180°/Lat) × 2 Views (dorsum/palm) × 2 Lateralities (left/right)] was presented once to the participant in the run. The order for each possible combination was pseudorandomized for each run and participant, and a maximum of either two haptic or two visual stimuli were presented in sequence. The experiment ended
with a fixation cross that lasted 15 sec (to capture the signal with the hemodynamic delay) and a subsequent final message “Experiment finished”.

Haptic stimuli consisted of four plastic hands [in two Views (dorsum/palm) and two Lateralities (left/right)] in neutral postures and fixed on plastic plates. The Styrofoam half sphere was also fixed on a plastic plate. The dimension of the plastic hands was 3 cm thickness / 9 cm width / 17 cm length. They were placed on an MR-compatible plate holder support build for the experiment (Fig. 2A), attached to the right side of the MR scanner bed. The plate holder support was adjusted according to each participants’ arm length prior to the MR acquisition. During the fMRI acquisition related to the mental rotation task, a trained experimenter was in the MR scanner room passing the haptic hand stimuli and the half-sphere to the participant as required by the protocol (Fig. 2B). The experimenter received auditory cues implemented in the code through MR-compatible headphones (which also provided hearing protection) indicating when and in which orientation each haptic stimulus should be positioned on and removed from the plate holder support, as well as when to place and remove the half sphere for visual trials. Visual stimuli consisted of images of Caucasian hands in neutral postures, covering a visual angle of about 13°. The participants in the MR scanner viewed the stimuli through a mirror attached to the head coil and oriented toward a translucent screen placed on the back of the scanner bore to which the stimuli were projected.

During a training session prior to the experiment, outside the MR scanner room, participants practiced a similar mental rotation task, comprised of visual and haptic hand stimuli, adapted to be performed with a laptop for practice and further instruction. During this training, the participants remained sitting and viewed the hand stimuli tilted by 45° with respect to the orientations used in the actual experiment. The haptic hand stimuli were also tilted by 45°. Also in the practice session, the haptic stimuli and the half sphere were provided by the experimenter in due course and blinded to the participants. Then, the participants were conducted to the MR scanner room, in which brain anatomical images were first acquired, followed by functional acquisitions of four runs of mental rotation of hands and one resting-state run (Fig. 1B). Due to time issues, one of the participants performed only three mental rotation runs and the resting-state run was not acquired from three participants.

2.3. MRI and psychometric data acquisition

We acquired functional and anatomical images using a Siemens Magnetom Prisma Fit 3 T scanner and a 64-channel head coil (Siemens, Erlangen, Germany) at the MR Center of the University Hospital, Lausanne, Switzerland. Functional images were acquired by using a T2*-weighted echo-planar imaging sequence, isotropic voxel size = 2 mm3, echo time/repetition time (TE/TR) = 30/2000 msec, 64 slices, simultaneous multislice factor = 2, field of view (FoV) = 192 mm2, flip angle = 80°, matrix size = 96 x 96, interleaved ascending acquisition, 2084 Hz bandwidth per pixel. The field of view was aligned parallel with the commissural line and included the whole cerebrum. Before each functional acquisition, dummy scans were acquired to establish steady-state magnetizations. The mental rotation runs comprised 210 volumes (7 min). Because the presentation code was designed to last 6 min 40 s, the last 10 volumes of the mental rotation runs were trimmed out of the data, resulting in a total of 200 functional volumes. The presentation code was triggered to the functional acquisition. Resting-state functional runs comprised of 180 volumes (6 min), in which participants were instructed to relax, breathe

![Fig. 1](image-url)
regularly, and not engage in any particular thought, while looking at a fixation cross on a white screen. Anatomical images were acquired using a T1-weighted magnetization prepared rapid gradient echo (MP2RAGE) sequence (Marques et al., 2010), isotropic voxel size = 1 mm³, FoV = 256 mm³, TE/TRMPRAGE = 2.9/5000 msec, 128 contiguous sagittal slices, inversion time (TI1)/flip angle = 700 msec/4°, TI2/flip angle = 2500 msec/5°, matrix size = 224 × 240, duration = 4 min.

During mental rotation runs, we also recorded the RT for trials with correct responses (RT > 6 sec were not recorded and the trial was labeled as incorrect). For each trial, we also recorded the sensory Modality (haptic or visual), Rotation (0°, Med, 180°, or Lat), View (dorsum or palm), and Laterality (left or right), as well as the onset of the presentation in a mental rotation run, and the run and trial indexes. Data were stored in .txt files to be evaluated post-hoc.

2.4. Data analysis

2.4.1. Behavioral data

We analyzed how RT for correct trials and accuracy depended on the factors Modality, Rotation, View, and Laterality. The accuracy was computed as the number of correct trials divided by the total number of trials and multiplied by 100% for each possible combination of Modality and Rotation factors. Statistical analyses were performed with RStudio (https://rstudio.com/). For RT, due to the unbalanced design (different number of correct answers for each subject) and data’s hierarchical structure (multiple RT measures nested within subject), we used linear mixed models to investigate main effects of each factor and their interactions with each other. In this model, Modality, Rotation, View, and Laterality were defined as fixed factors and subjects were defined as a random factor (Subject). Rotation was nested in Subject, but not the other factors due to insufficient levels to estimate variance (two levels each). To investigate the dependence of accuracy on the factors Modality and Rotation, we used a generalized linear model (library ‘lme4’) because of the skewed distribution of the data (other factors were not included in this model because of non-convergence). Main effects and interactions were considered significant according to a level of significance of .05. Post-hoc analyses were performed for pairwise comparisons between the levels of the factors (library ‘rstatix’). p-values were adjusted for multiple comparisons according to the Sidak method. As effect size estimates of the main effects and interactions, we computed the η² (library ‘effectsize’) for linear mixed models and the coefficient of determination (library ‘MuMIn’) for generalized linear mixed models.

2.4.2. MRI data preprocessing

All fMRI data acquired during mental rotation task and resting-state runs were preprocessed prior to statistical analysis. First, raw images were converted from DICOM (Digital Imaging and Communications in Medicine) to NIFTI (Neuroimaging Informatics Technology Initiative) format using the MRICron (https://www.nitrc.org/projects/mricron) software. The background noise in air regions of the MP2RAGE anatomical images was removed using a MATLAB script as proposed in (O’Brien et al., 2014). The next steps of standard preprocessing were performed with SPM12 (Statistical Parametric Mapping – http://www.fil.ion.ucl.ac.uk). Functional images were slice-time corrected using the middle slice as the reference slice. The six rigid-body parameters of head movement were estimated from the resulting images and spatial realignment to the generated mean functional image was performed for each run. Next, the anatomical image was coregistered to the space of the mean functional image and used to create a deformation field. This deformation field was used to spatially normalize preprocessed functional images of all participants to the Montreal Neurological Institute (MNI) stereotactic space. The resulting voxel size in the preprocessed functional images was 2 × 2 × 2 mm³. Finally, the processed functional images were spatially smoothed using an isotropic Gaussian kernel with 8-mm full width at half maximum.

For the statistical analyses described below, we designed three different general linear models aiming to disentangle different associations of brain activity with aspects of mental rotation of hands. Model 1 was used to investigate which brain regions show activity differences across rotations of hands and sensory stimuli, controlled for the influence of the response time. Model 2 was used to investigate which brain regions show a positive linear relationship between activity and rotation of hands (i.e., activity increases with the degree of rotation) for each sensory modality separately, controlled for the influence of the response time. Model 3 was used to...
investigate which brain regions show a linear relationship between activity and response time for each hand rotation separately. All analyses were performed using SPM12 and regions were automatically labeled using the Anatomy toolbox atlas (https://fil.ion.ucl.ac.uk/spm/ext/#Anatomy). For all models, beta values (regression weights) were estimated using two-level analyses and all mental rotation functional runs were concatenated in the design matrix because correct events could be null within a run for a participant in a combination Modality × Rotation. Additional regressors of no-interest were added to the model to remove the effect of runs. The event-related design allowed us to evaluate the RT on each trial, either to remove its influence (Models 1 and 2) or to examine its association with brain activity (Model 3). Addressing the influence of response time on brain activity in fMRI experiments is crucially important because variance in the BOLD signal can be strongly confounded by the RT (Yarkoni et al., 2009).

2.4.3. Model 1: differential brain activity across rotations for haptic and visual stimuli

In whole-brain and region-of-interest (ROI – described below) analyses, we investigated which brain regions show differential activation across Rotation and Modality, controlled for the influence of the response time. In the first-level analysis, we designed a matrix with eight unmodulated regressors, representing the trials for “0°”, “Med”, “180°”, and “Lat” Rotations for the two sensory Modalities separately, plus their associated modulated regressors. The unmodulated regressors were constructed with the onset of correct trials and constant duration, corresponding to the mean RT for each Modality separately and across correct trials for each participant. The modulated regressors were constructed by using the demeaned RT for each trial. This way, the parameter estimation of the unmodulated regressor was adjusted for the RT effect. Co-regressors of no-interest were included to the model, namely vectors representing View and Laterality, the six parameters of head movement, constant vectors for each run, and a linear trend vector representing practice effects (Berneiser et al., 2018). Betas (regression weights) were estimated for each Rotation and Modality, for all participants. Next, we individually computed linear combinations of the unmodulated regressors, based on the Kronecker product (Henson, 2015). These linear combinations were used to individually compute the interaction Modality × Rotation and the main effect of Modality and Rotation in Analyses of Variance (ANOVAs). Then, the individual contrast maps were fed to the second-level random-effects analysis and one-sample F-tests were applied. Such procedure constitutes a partitioned errors approach and is recommended for within-subject design because it controls for false positives with no concerns about non-sphericity (Henson, 2015). For whole-brain analysis, all resulting second-level maps were submitted to the threshold-free cluster enhancement (TFCE) approach (TFCE Toolbox – https://www.fil.ion.ucl.ac.uk/spm/ext/) with 5000 permutations, with a voxel-level inclusion threshold of p < .05, family-wise error (FWE)-corrected for multiple comparisons.

2.4.4. Model 2: positive linear relationship between brain activity and degree of Rotation

In a whole-brain analysis, we investigated which brain regions show a positive linear association between activity and Rotation, controlled for the influence of the response time. In the first-level analysis, we designed regressors representing correct trials for haptic and visual stimuli separately. The design matrix was constructed by specifying the unmodulated regressor and two parametric modulators, as described in (Mumford et al., 2015). The unmodulated regressor was specified by each trial onset and the mean RT as the constant duration for each Modality and participant. The first parametric regressor represented the RT modulation and it was constructed using the demeaned RT for each trial (and each Modality separately). The second parametric regressor represented the rotation degree, labeled 0, 90, and 180 for the computation of the linear relationship (“Med” was here labeled “90”). For this model, lateral rotations (Lat) were not considered because the cognitive load in mental rotation of hands is thought to increase with the degree of rotation reaching its maximum at 180° and to decrease for higher angles until returning to 0° (Cooper & Shepard, 1975). In SPM, specifying the RT modulator prior to the rotation degree modulator means that the rotation degree is orthogonalized with respect to the unmodulated regressor and the RT (third row in Fig. 3 of Mumford et al., 2015). In practice, this design allows the interpretation that the estimated modulation parameter of the rotation degree as unique stimulus activation, adjusted for the RT effect. Co-regressors of no-interest were defined exactly as in Model 1. Individual contrast maps representing the parameter estimates for the rotation degree (the second parametric modulator) for each Modality were fed to the second-level random-effects analysis using a one-sample t-test. Positive thresholded maps were obtained using TFCE with 5000 permutations (Smith & Nichols, 2009), with voxel-level inclusion thresholds of p < .0005 for haptic and p < .05 for visual stimuli and for the difference in estimates of linear association activity × Rotation between haptic and visual stimuli, FWE-corrected for multiple comparisons.

2.4.5. Model 3: association of brain activity and RT for haptic and visual stimuli and within degrees of Rotation

In whole-brain and ROI (described below) analyses, we investigated the association of brain activity and RT for haptic and visual stimuli separately and within each degree of Rotation. For the first-level analysis, we used the individual beta maps estimated in Model 1 for the modulated regressors representing RT on each trial for each Rotation and Modality separately. The individual contrast maps were fed to the second-level random-effects analysis and one-sample t-tests were applied for each combination Rotation × Modality. This way, we could infer which brain regions supported (negative betas) or hindered (positive betas) performance of mental rotation of hands for haptic and visual stimuli and within each degree of Rotation. For whole-brain analysis, all resulting second-level maps were submitted to the TFCE with 5000 permutations, with a voxel-level inclusion threshold of p < .05, FWE-corrected for multiple comparisons.
2.4.6. Analyses of regions of interest (ROIs)
We analyzed the dependence of brain activity across Rotations and sensory Modalities (Model 1) and the association between brain activity and RT within Rotations (Model 3) within predetermined ROIs. In comparison with the whole-brain mapping, the ROI analysis reduces the number of voxel-wise multiple comparisons and may reveal effects that would otherwise remain undetected.

For Model 1, a total of 21 regions were defined using MarsBaR (http://marsbar.sourceforge.net) (Table 1). Eight-mm-radius spherical ROIs were centered in coordinates obtained from independent sources to avoid circular analysis (Kriegeskorte et al., 2009). Thirteen of these coordinates were extracted from a meta-analytic study (Tomasino & Gremese, 2016) reporting a brain network related to mental rotation. These ROIs represented the left and right intraparietal sulcus (IPS), left and right premotor cortex (PMC), left and right inferior occipital gyrus (IOG), left and right inferior frontal gyrus (IFG), supplementary motor cortex (SMA), left and right middle frontal gyrus (MFG), left fusiform gyrus, and left lingual gyrus. Further details of the ROI definition using this study are described in the section “Detailed procedure for ROI definition from Tomasino and Gremese (2016)” of the Supplementary material. Four other ROIs were created using coordinates extracted from Bingel et al. (2004): the left and right primary (S1) and secondary somatosensory cortex (S2). The S1 and S2 coordinates were transformed into the MNI space using the function tal2icbm_spm (http://brainmap.org/icbm2tal/). ROIs representing the left and right anterior insula (ant insula) and supramarginal gyrus (SMG), regions commonly reported in fMRI studies on mental rotation of hands (Berneiser et al., 2018; Kashuk et al., 2017; Kitada et al., 2010; Perruchoud et al., 2016; Vingerhoets et al., 2002; Zapparoli et al., 2014), were also created using the peak values of maps extracted from Neurosynth, an automated meta-analytic platform for fMRI studies [http://www.neurosynth.org on 3/26/2021 (Yarkoni et al., 2011)]. No part of the study analyses was pre-registered prior to the research being conducted.

For Model 3, besides investigating the whole-brain association between RT and activation (described above), we also investigated the association between RT and activation of the default mode network (DMN). DMN activation is widely accepted to be related to performance detriment on an externally-oriented attentional task (Andrews-Hanna et al., 2014; Hinds et al., 2013; Kelly et al., 2008). Because the anatomical position of the ROIs was individually defined using resting-state fMRI data, this analysis was performed only with subjects who performed the resting-state acquisition (N = 28). First, the preprocessed resting-state images were included as inputs for the independent component analysis (ICA) estimation using the Gift toolbox (http://mialab.mrn.org/software/gift), using a predefined number of 25 components. Next, the component representing the dorsal DMN was identified and subject-specific masks comprised of four 6-mm-radius spherical ROIs (including the posterior cingulate gyrus, medial prefrontal gyrus, and bilateral angular gyrus) were created using Personode [https://www.nitrc.org/projects/personode (Pamplona et al., 2020)]. For means of comparison, the same analysis was made using non-individualized ROIs, based on a DMN mask created from the peak coordinates of the UKBiobank ICA estimation (Miller et al., 2016).

Finally, beta estimates were averaged across voxels within each ROI, computed in the general linear models from regressors of interest of Models 1 and 3, separately for each participant, Modality, and Rotation using MarsBaR. Next, using R, we computed two-way repeated-measures ANOVAs to examine the dependence of activity in each ROI and the factors Modality and Rotation. We report the main effects of Rotation.

Fig. 3 – Effects of mental rotation of hands in the RT (A) and accuracy (B) were observed for both haptic and visual stimuli. Asterisks represent significant differences in post-hoc tests following linear mixed model analyses corrected for multiple comparisons using the Sidak correction (****p < .0001, ***p < .001, *p < .05). Results for haptic and visual stimuli are shown in red and blue, respectively. RT = response time, Med = medial, Lat = lateral.
only for the ROIs with nonsignificant interactions, together with the main effects of Modality. Because of the multiple comparisons across ROIs, p-values for interactions and main effects were corrected according to the Benjamini–Hochberg false-discovery rate (FDR) procedure. Partial eta-squared values (\(\eta^2\)) were computed (library 'DescTools') as effect sizes of interactions and main effects. Post-hoc analyses of significant main effects and interactions Modality \(\times\) Rotation were computed, p-values corrected for multiple comparisons using the Sidak method. Effect sizes for the post-hoc analysis were computed through the difference between the two estimated marginal means (library 'emmeans') (Lenth et al., 2018). All obtained results (except by individual-level whole-brain maps) and analysis codes are available on the public GitHub repository: https://github.com/gustavopamplona/TacMentRot_public_data.

### 3. Results

#### 3.1. Behavioral results

Effects of Rotation were observed in the RT for both haptic and visual stimuli (Fig. 3A, Tables 2 and S1). From a linear mixed model analysis considering the RT as a function of four factors (Modality, Rotation, View, and Laterality), we observed significant three-way [Modality \(\times\) Rotation \(\times\) Laterality: \(F(3,3731) = 2.90, \eta^2 = .0023, p = .03\)] and two-way interactions [Modality \(\times\) Rotation: \(F(3,3732) = 20.3, \eta^2 = .02, p < .0001;\) Rotation \(\times\) View: \(F(3,3731) = 16.8, \eta^2 = .01, p < .0001;\) Rotation \(\times\) Laterality: \(F(3,3731) = 4.28, \eta^2 = .003, p = .005\)], and main effects [Modality: \(F(1,3732) = 1947, \eta^2 = .34, p < .0001;\) Rotation: \(F(3,90.1) = 49.7, \eta^2 = .62, p < .0001;\) View: \(F(3,186.2) = 37, \eta^2 = .28, p < .0001\)] and accuracy (%). Accuracy (%) across rotations and modalities. For RT, we show average (and standard deviation) values for correct trials across subjects for each combination of conditions and collapsed for runs. Gray cells indicate descriptive statistics collapsed for haptic and visual stimuli separately. For accuracy, we show median (and the first and third quartile) values across subjects and collapsed for runs, view, and laterality.

### Table 1 – Regions of interest (ROIs) for Model 2 identified based on (a) Tomasino & Gremsme (2016); (b) Bingel et al. (2004); and (c) Yarkoni et al. (2011).

<table>
<thead>
<tr>
<th>Brain region (reference)</th>
<th>Abbreviation</th>
<th>Hemisphere</th>
<th>Center (x,y,z)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intraparietal sulcus (a)</td>
<td>IPS</td>
<td>Left</td>
<td>–18, –64, 52</td>
</tr>
<tr>
<td>Premotor cortex (a)</td>
<td>PMC</td>
<td>Left</td>
<td>–26, –4, 56</td>
</tr>
<tr>
<td>Inferior occipital cortex (a)</td>
<td>IOC</td>
<td>Left</td>
<td>–48, –70, –6</td>
</tr>
<tr>
<td>Inferior frontal gyrus (a)</td>
<td>IFG</td>
<td>Right</td>
<td>–44, 26, 16</td>
</tr>
<tr>
<td>Supplementary motor area (a)</td>
<td>SMA</td>
<td>Right</td>
<td>52, 10, 24</td>
</tr>
<tr>
<td>Anterior insula (c)</td>
<td>Ant Insula</td>
<td>Medial</td>
<td>4, 14, 48</td>
</tr>
<tr>
<td>Medial frontal gyrus (a)</td>
<td>MFG</td>
<td>Right</td>
<td>–44, 32, 28</td>
</tr>
<tr>
<td>Fusiform gyrus (a)</td>
<td>–</td>
<td>Left</td>
<td>–30, –54, –12</td>
</tr>
<tr>
<td>Lingual gyrus (a)</td>
<td>–</td>
<td>Left</td>
<td>–15, –69, –1</td>
</tr>
<tr>
<td>Primary somatosensory cortex (b)</td>
<td>S1</td>
<td>Right</td>
<td>–38, 37, 57</td>
</tr>
<tr>
<td>Secondary somatosensory cortex (b)</td>
<td>S2</td>
<td>Right</td>
<td>–45, –16, 14</td>
</tr>
<tr>
<td>Supramarginal gyrus (c)</td>
<td>SMG</td>
<td>Right</td>
<td>49, –17, 16</td>
</tr>
</tbody>
</table>

### Table 2 – Average response time (RT) across rotations (0°, Med, 180°, and Lat) for each factor (Modality, View, and Laterality) and accuracy (%) across rotations and modalities. For RT, we show average (and standard deviation) values for correct trials across subjects for each combination of conditions and collapsed for runs. Gray cells indicate descriptive statistics collapsed for haptic and visual stimuli separately. For accuracy, we show median (and the first and third quartile) values across subjects and collapsed for runs, view, and laterality.

<table>
<thead>
<tr>
<th>Modality</th>
<th>View</th>
<th>Laterality</th>
<th>Med</th>
<th>180°</th>
<th>Lat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Haptic</td>
<td>Palm</td>
<td>Left</td>
<td>2.81 (.58)</td>
<td>3.12 (.71)</td>
<td>3.36 (.79)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Right</td>
<td>3.06 (.92)</td>
<td>3.01 (.95)</td>
<td>3.28 (.77)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>2.84 (.58)</td>
<td>3.09 (.55)</td>
<td>3.43 (.62)</td>
</tr>
<tr>
<td>Visual</td>
<td>Palm</td>
<td>Left</td>
<td>1.74 (.47)</td>
<td>1.71 (.50)</td>
<td>2.55 (.80)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Right</td>
<td>1.67 (.53)</td>
<td>1.59 (.50)</td>
<td>2.29 (.76)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>1.60 (.44)</td>
<td>1.73 (.50)</td>
<td>2.40 (.63)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Accuracy (%)</th>
<th>Haptic</th>
<th>Total</th>
<th>93.8 (87.5–100)</th>
<th>93.8 (84.4–100)</th>
<th>91.7 (81.2–93.8)</th>
<th>93.8 (93.8–100)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Visual</td>
<td>Total</td>
<td>100 (93.8–100)</td>
<td>100 (100–100)</td>
<td>93.8 (87.5–100)</td>
<td>100 (93.8–100)</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 4 – Significant interactions Modality × Rotation (Model 1) were observed in the activity of sensorimotor regions; here, we show regions that exhibited opposite effects depending on the Modality (higher activation for rotated haptic stimuli and higher deactivation for rotated visual stimuli). (A) The whole-brain analysis showed that the left secondary somatosensory cortex (S2) exhibited significant interaction Modality × Rotation. Warm colors represent the intensity of F-values from a group TFCE analysis. (B) In addition to the left S2, ROI analyses identified that also the right S2, the left supramarginal gyrus...
F(1,3731) = 4.99, $\eta^2 = .0013$, $p = .026$; Laterality: F(1,3731) = 17.7, $\eta^2 = .005$, $p < .0001$. In general terms, shorter RT were observed for visual compared to haptic stimuli, for right-compared to left-lateralized hands, and for dorsum compared to palm views. Importantly, post-hoc analyses showed longer RT for awkward hand Rotations (Lat) only for visual stimuli. Furthermore, expected Rotation-related RT differences were observed for all pairwise comparisons between Rotations (all ps < .05), except for the differences Lat minus 0° for haptic stimuli, and for the difference Med minus 0° for visual stimuli.

From a generalized linear mixed model analysis considering the accuracy as a function of two factors (Modality and Rotation), we observed the significant interaction Modality $\times$ Rotation [$X^2(3) = 13.7, R^2 = .09, p = .003$], as well as main effects of Modality [$X^2(1) = 7.09, R^2 = .09, p = .008$] and Rotation [$X^2(3) = 10.7, R^2 = .06, p = .013$] (Fig. 3B, Tables 2 and S2). Post-hoc analysis showed expected Rotation-related accuracy differences: lower accuracy for 180° compared to 0° for both stimuli, for 180° compared to Med for visual stimuli, and for Lat compared to Med for visual stimuli (all ps < .05). In other words, higher accuracy was obtained for visual compared to haptic stimuli, for less rotated compared to more rotated ones, and for a comfortable posture (Med) compared to an awkward one (Lat) for visual stimuli only.

### 3.2 Differential rotation-related brain activity: activation for haptic and deactivation for visual mental rotation of hands (interactions in Model 1)

For Model 1, we found brain regions whose activation showed a significant two-way interaction Modality $\times$ Rotation in ANOVA for whole-brain and ROI analyses. Here, we report regions whose Rotation effects were observed as activations for haptic stimuli and deactivations for visual stimuli. Among them, the left secondary somatosensory cortex followed this pattern, detected in both whole-brain (peak coordinates = $-50, -14, 16$; peak t-value = 3.70, 241 voxels in the cluster, TFCE FWE-corr. p-value for combined peak-cluster-level < .001) (Fig 4A) and ROI analyses [$F(3,90) = 11.1, \eta^2 = .27, p < .0001$] (Fig. 4B, Table 3). Other ROIs showed a similar pattern: the right secondary somatosensory cortex [$F(3,90) = 6.13, \eta^2 = .17, p = .005$] and the left supramarginal gyrus [$F(3,90) = 4.36, \eta^2 = .13, p = .016$] (Fig. 4B). In general, post-hoc analysis indicated that, for haptic stimuli, Rotation-related activation in these regions is evident for any Rotation; in contrast, for visual stimuli, Rotation-related deactivation in these regions is only evident for highly rotated stimuli and for the awkward posture (Lat).

### 3.3 Differential rotation-related brain activity: activation for haptic and visual mental rotation of hands (interactions in Model 1)

This section illustrates regions that showed activation (and not deactivation) for haptic and visual stimuli and significant two-way interactions Modality $\times$ Rotation in Model 1. Post-hoc analysis indicated regions showing Rotation-related activation differences for both Modalities (Fig. 5A, Table 4): the left intraparietal sulcus [$F(3,90) = 5.81, \eta^2 = .16, p = .005$], the right anterior insula [$F(3,90) = 3.25, \eta^2 = .10, p = .04$], and left [$F(3,90) = 3.79, \eta^2 = .11, p = .023$] and right premotor cortex [$F(3,90) = 4.20, \eta^2 = .12, p = .015$]. Post-hoc analysis also indicated regions showing differences Rotation-related activation differences only for visual stimuli (Fig. 5B, Table 4): the left [$F(3,90) = 5.46, \eta^2 = .15, p = .007$] and right inferior occipital gyrus [$F(3,90) = 4.92, \eta^2 = .14, p = .011$], the supplementary motor area [$F(3,90) = 4.29, \eta^2 = .13, p = .015$], and the right intraparietal sulcus [$F(3,90) = 4.71, \eta^2 = .14, p = .012$].

### 3.4 Association between brain activity and rotation for haptic and visual mental rotation of hands (Model 2)

The interaction results from Model 1 shown in section 3.3 can be complemented with the results from Model 2, which shows distinct patterns of positive linear relationship between brain activation and Rotation for haptic and visual stimuli. While the ANOVA results (Model 1) represent differences across conditions (within Modality or Rotation), Model 2 reveals brain regions whose activation increased linearly with Rotation, separately for each Modality. The left premotor cortex was positively associated with mental rotation of haptic stimuli (Fig. 6A, Table 5) and the right superior occipital gyrus (or intraparietal sulcus) were positively associated with mental rotation of visual stimuli (Fig. 6B, Table 5). Therefore, mental rotation of haptic and visual stimuli was positively associated with motor cortex and visual cortex regions, respectively. The activation in the premotor and the occipital cortexes was also found to differ across conditions by Model 1 (Fig. 5A and B, respectively); however, Model 2 shows that the increase in activation in these regions is also linear. Fig. S1 and Table S3 show significant brain clusters for the difference in estimates of linear association activity $\times$ Rotation between haptic and visual stimuli.

### 3.5 Common effects of rotation in brain activity for haptic and visual mental rotation of hands (main effects in Model 1)

The ANOVA for whole-brain and ROI analyses further revealed brain regions whose activation showed significant main effects of Rotation in Model 1 (and no significant two-way interaction Modality $\times$ Rotation). Namely, these effects were found in the middle occipital gyrus, as well as in the fusiform gyrus, for the whole-brain analysis (Fig. 7A and Table 6). ROI analysis also showed main effects of Rotation in the left fusiform gyrus [$F(3,90) = 11.8, \eta^2 = .28, p < .0001$], left lingual gyrus [$F(3,90) = 6.61, \eta^2 = .18, p = .0016$] and left anterior insula [$F(3,90) = 5.14, \eta^2 = .15, p = .006$] (Fig. 7B, Table 7). In addition, among these regions, we observed significant main effects of Modality in the left fusiform gyrus (SMG), and the left primary somatosensory cortex (S1) exhibited the same pattern (defined regions of interest are shown on top). Results for haptic and visual stimuli are shown in red and blue, respectively. Asterisks represent significant differences in post-hoc tests following repeated-measures ANOVAs corrected for multiple comparisons using the Sidak method (***p < .0001, ***p < .001, **p < .01, *p < .05). Med = medial, Lat = lateral.
Table 3 – Inferential statistics from ROI analysis for regions showing significant interactions Modality × Rotation (Model 1) and inverted effects of rotation across modalities (greater activation for rotated haptic stimuli and lower activation for rotated visual stimuli). Bold cells show inferential statistics of significant interactions (Modality × Rotation) following two-way repeated-measures ANOVAs (p < .05, FDR-corrected for multiple comparisons, i.e., the number of ROIs). Results from post-hoc analyses show significant pairwise comparisons across rotations and modalities (p < .05, adjusted for multiple comparisons using the Sidák correction). DoF = degrees of freedom. S1/S2 = primary/secondary somatosensory cortex, SMG = supramarginal gyrus, Med = medial, Lat = lateral.

<table>
<thead>
<tr>
<th>Modality</th>
<th>Rotation</th>
<th>Effect size</th>
<th>DoF</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Left S2 – interaction Modality × Rotation – F(3,90) = 11.1, η² = .27, p &lt; .0001</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0°–Med</td>
<td>–.41</td>
<td>178</td>
<td>–4.52</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>0°–180°</td>
<td>–.29</td>
<td>178</td>
<td>–3.18</td>
<td>.010</td>
</tr>
<tr>
<td>Visual</td>
<td>0°–180°</td>
<td>0.32</td>
<td>178</td>
<td>3.51</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>0°–Lat</td>
<td>0.29</td>
<td>178</td>
<td>3.23</td>
<td>.009</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>0.40</td>
<td>95.4</td>
<td>3.93</td>
<td>&lt;.0002</td>
</tr>
<tr>
<td></td>
<td>180°</td>
<td>0.51</td>
<td>95.4</td>
<td>5.09</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>0.48</td>
<td>95.4</td>
<td>4.80</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td><strong>Right S2 – Interaction Modality × Rotation – F(3,90) = 6.13, η² = .17, p = .005</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0°–Med</td>
<td>–.41</td>
<td>179</td>
<td>–5.07</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>0°–180°</td>
<td>–.27</td>
<td>179</td>
<td>–3.31</td>
<td>.007</td>
</tr>
<tr>
<td>Visual</td>
<td>0°–180°</td>
<td>0.23</td>
<td>179</td>
<td>2.80</td>
<td>.03</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>0.47</td>
<td>99.5</td>
<td>4.77</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>180°</td>
<td>0.44</td>
<td>99.5</td>
<td>4.51</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>0.44</td>
<td>99.5</td>
<td>4.49</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td><strong>Left SMG – interaction Modality × Rotation – F(3,90) = 4.36, η² = .13, p = .016</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0°–Med</td>
<td>–.25</td>
<td>180</td>
<td>–2.99</td>
<td>.19</td>
</tr>
<tr>
<td></td>
<td>0°–180°</td>
<td>0.32</td>
<td>180</td>
<td>3.84</td>
<td>&lt;.010</td>
</tr>
<tr>
<td>Visual</td>
<td>0°–180°</td>
<td>0.47</td>
<td>87.1</td>
<td>4.49</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>0.82</td>
<td>87.1</td>
<td>7.85</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>180°</td>
<td>0.86</td>
<td>87.1</td>
<td>8.18</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>0.68</td>
<td>87.1</td>
<td>6.50</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td><strong>Left S1 – interaction Modality × Rotation – F(3,90) = 4.56, η² = .13, p = .013</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0°–Med</td>
<td>–.26</td>
<td>179</td>
<td>–3.33</td>
<td>.006</td>
</tr>
<tr>
<td></td>
<td>0°–Lat</td>
<td>–.22</td>
<td>179</td>
<td>–2.77</td>
<td>.04</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>1.19</td>
<td>61.2</td>
<td>8.08</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>180°</td>
<td>1.24</td>
<td>61.2</td>
<td>10.8</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>1.28</td>
<td>61.2</td>
<td>11.2</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>

[F(1,30) = 37.5, η² = .56, p < .0001] and in the left lingual gyrus [F(1,30) = 6.53, η² = .18, p = .028]. Specifically, post-hoc analyses showed that the left fusiform gyrus was more active for visual compared to haptic stimuli [t(30) = 6.12, d = 41, p < .0001], while the left lingual gyrus was more active for haptic compared to visual stimuli [t(30) = 2.56, d = 26, p = .016]. Main effect of Modality was not observed for the activation in the left anterior insula. Altogether, these main effects suggest that fusiform and lingual gyri are involved in mental rotation of hands regardless of the stimuli, but to different extents depending on the sensory nature of the stimuli. All significant main effects of Modality and Rotation for the ANOVA performed in the ROI analysis (including the already reported regions with significant two-way interaction Modality × Rotation) are shown in Tables S4 and S5, respectively. Main effect of Modality for the whole-brain analysis is also shown in Figure S2.

3.6. Performance-related brain activity for haptic and visual mental rotation of hands (Model 3)

Finally, for Model 3, we found regions whose activation was associated with performance in haptic and visual mental rotation of hands in a whole-brain analysis. Specifically, we observed that a bilateral network consisting of sensorimotor regions (postcentral, precentral, and premotor gyri) was negatively associated with RT (i.e., associated with better performance) for highly rotated haptic stimuli (Fig. 8A, Table 8). Another network consisting of occipital regions was positively associated with RT (i.e., associated with worse performance) for rotated visual stimuli, observed mainly in the awkward posture (Lat) (Fig. 8B and S3, Table 8). An additional ROI analysis indicated a significant interaction Modality × Rotation [F(3,81) = 4.48, η² = .14, p = .006] in the DMN activation. Specifically, post-hoc analysis revealed that the association
between DMN activity and RT is lower for highly rotated [0°−180°; effect size = .36, t(159) = 3.28, p = .0013] and for the awkward posture [0°−Lat, effect size = .29, t(159) = 2.68, p = .008] compared to unrotated visual stimuli (Fig. 8C). A non-personalized definition of the DMN did not lead to a significant interaction Modality × Rotation (p > .8).

4. Discussion

In this fMRI study, we mapped and characterized brain activity related to the mental rotation of haptically- and visually-presented hands. To the best of our knowledge, this is
Table 4 – Inferential statistics from ROI analysis for regions showing significant interactions Modality × Rotation (Model 1) and positive effects of rotation on activation for either both modalities or only for visual Modality (according to post-hoc analyses). Bold cells show inferential statistics of significant interactions (Modality × Rotation) following two-way repeated-measures ANOVAs (p < .05, FDR-corrected for multiple comparisons, i.e., the number of ROIs). Results from post-hoc analyses show significant pairwise comparisons across Rotations and Modalities (p < .05, adjusted for multiple comparisons using the Sidak correction). DoF = degrees of freedom, PMC = premotor cortex, IPS = intraparietal sulcus, IOG = inferior occipital gyrus, SMA = supplementary motor area, Med = medial, Lat = lateral.

<table>
<thead>
<tr>
<th>Modality</th>
<th>Rotation</th>
<th>Effect size</th>
<th>DoF</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left PMC – interaction Modality × Rotation</td>
<td>F(3,90) = 3.79, ( \eta^2 = .11, p = .023 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0′–Med</td>
<td>–.24</td>
<td>171</td>
<td>–3.47</td>
<td>.004</td>
</tr>
<tr>
<td></td>
<td>0′–180°</td>
<td>–.20</td>
<td>171</td>
<td>–2.86</td>
<td>.028</td>
</tr>
<tr>
<td>Visual</td>
<td>0′–180°</td>
<td>–.27</td>
<td>171</td>
<td>–4.02</td>
<td>.0005</td>
</tr>
<tr>
<td></td>
<td>Med–180°</td>
<td>–.23</td>
<td>171</td>
<td>–3.41</td>
<td>.005</td>
</tr>
<tr>
<td></td>
<td>180°–Lat</td>
<td>.18</td>
<td>171</td>
<td>2.72</td>
<td>.04</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>0′</td>
<td>.25</td>
<td>67.2</td>
<td>2.94</td>
<td>.004</td>
</tr>
<tr>
<td></td>
<td>Med</td>
<td>.45</td>
<td>67.2</td>
<td>5.21</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>180°</td>
<td>.17</td>
<td>67.2</td>
<td>2.02</td>
<td>.05</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>.33</td>
<td>67.2</td>
<td>3.86</td>
<td>.0003</td>
</tr>
<tr>
<td>Right PMC – interaction Modality × Rotation</td>
<td>F(3,90) = 4.20, ( \eta^2 = .12, p = .015 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0′–Med</td>
<td>–.25</td>
<td>180</td>
<td>–3.57</td>
<td>.0027</td>
</tr>
<tr>
<td></td>
<td>0′–180°</td>
<td>–.20</td>
<td>180</td>
<td>–2.84</td>
<td>.03</td>
</tr>
<tr>
<td>Visual</td>
<td>0′–Lat</td>
<td>–.23</td>
<td>180</td>
<td>–3.38</td>
<td>.005</td>
</tr>
<tr>
<td></td>
<td>180°–Lat</td>
<td>.28</td>
<td>180</td>
<td>–4.02</td>
<td>.0005</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>0′</td>
<td>.21</td>
<td>111</td>
<td>2.80</td>
<td>.006</td>
</tr>
<tr>
<td></td>
<td>Med</td>
<td>.44</td>
<td>111</td>
<td>5.91</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>.30</td>
<td>111</td>
<td>4.06</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Left IPS – interaction Modality × Rotation</td>
<td>F(3,90) = 5.81, ( \eta^2 = .16, p = .005 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0′–Med</td>
<td>–.31</td>
<td>180</td>
<td>–3.26</td>
<td>.008</td>
</tr>
<tr>
<td></td>
<td>0′–180°</td>
<td>–.42</td>
<td>180</td>
<td>–4.44</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Visual</td>
<td>0′–Lat</td>
<td>–.48</td>
<td>180</td>
<td>–5.10</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Med–180°</td>
<td>–.29</td>
<td>179</td>
<td>–2.97</td>
<td>.02</td>
</tr>
<tr>
<td></td>
<td>180°–Lat</td>
<td>.31</td>
<td>179</td>
<td>3.20</td>
<td>.010</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>.44</td>
<td>89.4</td>
<td>3.69</td>
<td>.0004</td>
</tr>
<tr>
<td>Right anterior insula – interaction Modality × Rotation</td>
<td>F(3,90) = 3.25, ( \eta^2 = .10, p = .04 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haptic</td>
<td>0′–Med</td>
<td>–.30</td>
<td>179</td>
<td>–3.12</td>
<td>.013</td>
</tr>
<tr>
<td></td>
<td>0′–180°</td>
<td>–.30</td>
<td>179</td>
<td>–3.10</td>
<td>.013</td>
</tr>
<tr>
<td>Visual</td>
<td>0′–Lat</td>
<td>–.29</td>
<td>179</td>
<td>–2.97</td>
<td>.020</td>
</tr>
<tr>
<td></td>
<td>Med–180°</td>
<td>–.31</td>
<td>179</td>
<td>3.20</td>
<td>.010</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>.28</td>
<td>105</td>
<td>2.61</td>
<td>.010</td>
</tr>
<tr>
<td>Left IOG – interaction Modality × Rotation</td>
<td>F(3,90) = 5.46, ( \eta^2 = .15, p = .007 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visual</td>
<td>0′–180°</td>
<td>–.45</td>
<td>180</td>
<td>–2.52</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Med–180°</td>
<td>–.47</td>
<td>180</td>
<td>–2.74</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Med–Lat</td>
<td>–.25</td>
<td>180</td>
<td>2.30</td>
<td>.04</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>0′</td>
<td>–.58</td>
<td>77.7</td>
<td>–4.65</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Med</td>
<td>–.36</td>
<td>77.7</td>
<td>–2.88</td>
<td>.005</td>
</tr>
<tr>
<td></td>
<td>180°</td>
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<td>77.7</td>
<td>–7.18</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>–.64</td>
<td>77.7</td>
<td>–5.10</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Right IOG – interaction Modality × Rotation</td>
<td>F(3,90) = 4.92, ( \eta^2 = .14, p = .011 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visual</td>
<td>0′–180°</td>
<td>–.43</td>
<td>176</td>
<td>–4.00</td>
<td>.0006</td>
</tr>
<tr>
<td></td>
<td>0′–Lat</td>
<td>–.32</td>
<td>176</td>
<td>–2.96</td>
<td>.021</td>
</tr>
<tr>
<td></td>
<td>Med–180°</td>
<td>–.42</td>
<td>176</td>
<td>–3.93</td>
<td>.0007</td>
</tr>
<tr>
<td></td>
<td>Med–Lat</td>
<td>–.31</td>
<td>176</td>
<td>–2.89</td>
<td>.026</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>0′</td>
<td>–.81</td>
<td>80.8</td>
<td>–5.46</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Med</td>
<td>–.72</td>
<td>80.8</td>
<td>–4.83</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>180°</td>
<td>–1.28</td>
<td>80.8</td>
<td>–8.65</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>Lat</td>
<td>–1.05</td>
<td>80.8</td>
<td>–7.08</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Right IPS – interaction Modality × Rotation</td>
<td>F(3,90) = 4.71, ( \eta^2 = .14, p = .012 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visual</td>
<td>0′–180°</td>
<td>–.37</td>
<td>175</td>
<td>–3.78</td>
<td>.0013</td>
</tr>
<tr>
<td></td>
<td>Med–180°</td>
<td>–.41</td>
<td>175</td>
<td>–4.15</td>
<td>.0003</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>.38</td>
<td>76.4</td>
<td>2.65</td>
<td>.010</td>
</tr>
<tr>
<td>SMA – interaction Modality × Rotation</td>
<td>F(3,90) = 4.29, ( \eta^2 = .13, p = .015 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visual</td>
<td>0′–180°</td>
<td>–.28</td>
<td>180</td>
<td>–3.05</td>
<td>.016</td>
</tr>
<tr>
<td></td>
<td>Med–180°</td>
<td>–.41</td>
<td>180</td>
<td>–4.44</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td></td>
<td>180°–Lat</td>
<td>.26</td>
<td>180</td>
<td>2.79</td>
<td>.03</td>
</tr>
<tr>
<td>Haptic – visual</td>
<td>Med</td>
<td>.37</td>
<td>105</td>
<td>3.59</td>
<td>.0005</td>
</tr>
</tbody>
</table>
the first study that investigated the brain correlates of touch-mediated mental rotation of hands. The study also dissociated the effects of the response time on brain activity during mental rotation of hands using trial-by-trial modeling. We found that:

1) We observed activation for haptic and deactivation for visual mental rotation of hands in the sensorimotor network (S1, S2, and SMG).

2) Other regions showed differential activation between haptic and visual mental rotation of hands. Rotation-related activation was observed in the left intraparietal sulcus, right anterior insula and premotor cortex for both modalities, but activation due to a low rotation was only observed for haptic stimuli. The inferior occipital gyrus, supplementary motor area and right intraparietal sulcus was only associated with visual mental rotation of hands. The association between brain activation and rotation was linear in the left premotor cortex for haptic stimuli and in the right intraparietal sulcus for visual stimuli.

3) Common effects of rotation in brain activity for haptic and visual mental rotation of hands in the left anterior insula, as well as in the middle occipital, lingual and fusiform gyri. While activity in the lingual gyrus was higher for haptic than visual stimuli, the opposite was observed in the fusiform gyrus.

4) Activity in the sensorimotor cortex was also positively associated with faster mental rotation of haptic stimuli. Activity in the occipital cortex and in the DMN was associated with slower mental rotation of visual stimuli.

4.1. Behavioral results

In line with previous findings regarding mental rotation of haptic (Kitada et al., 2009; Rangel et al., 2010) and visual hand stimuli (Cooper & Shepard, 1975; Marmor & Zaback, 1976; Sekiyama, 1982), we found that, for both sensory modalities, a longer RT was associated with a greater disparity of the hand’s upright orientation. Such a result is typical for mental rotation of body parts (Cooper & Shepard, 1975; de Lange et al., 2006; Rangel et al., 2010; Vingerhoets et al., 2002) and is assumed to reflect the influence of biomechanical constraints on imagined hand movements (Schwoebel et al., 2001). The present results are consistent with previous findings showing shorter RT for the mental rotation of visually-versus haptically-presented hands (Kitada et al., 2009; Rangel et al., 2010). Object

**Table 5** – Brain regions in which there is a positive linear relationship (Model 1) between brain activation (beta) and the values of Rotation [0°, 90° (Med), and 180°] for haptic and visual stimuli.

<table>
<thead>
<tr>
<th>Region Label</th>
<th>Extent (mm³)</th>
<th>t-value</th>
<th>MNI Coordinates</th>
<th>TFCE p-value for combined peak-cluster-level</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>FWE-corr.</td>
</tr>
<tr>
<td>Haptic stimuli</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left middle frontal gyrus</td>
<td>1584</td>
<td>3.63</td>
<td>-24 -6 56</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Right superior occipital gyrus</td>
<td>3696</td>
<td>3.01</td>
<td>26 -68 34</td>
<td>.026</td>
</tr>
<tr>
<td>Visual stimuli</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Fig. 6** – Brain regions in which there was a positive linear relationship (Model 2) between brain activation (beta) and the values of Rotation [0°, 90° (Med), and 180°] for haptic (A) and visual (B) stimuli. Surface-rendered images and axial slices are shown at top and bottom, respectively. Warm colors represent the intensity of t-values from a group TFCE analysis.
recognition via haptic stimuli is localized, sequential, and integrative by nature, compared to the quasi-instantly detection visual perception. Despite this obvious difference in the RT for visual and haptic stimuli, effects due to Rotation can be observed independently on the sensory modality. Taken together, these effects support that participants were engaged in both tasks and used mental imagery strategies for both sensory modalities (Kosslyn et al., 2001). Additionally, the findings agree with previous studies in terms of shorter RT for right-versus left-lateralized hands (Ni Choisdealbha et al., 2011; Zapparoli et al., 2014) and for dorsum-versus palm-view hands (Ionta & Blanke, 2009; Zapparoli et al., 2014).

We observed other notable differences between haptically- and visually-based mental rotation of hands. The RT difference between medial posture and no rotation was significant for haptic but not for visual stimuli. Furthermore, accuracy was higher for small than large rotations for visual compared to haptic stimuli. Also, only for visual stimuli, the RT was shorter and the accuracy was higher for medial compared to lateral postures. In other words, we confirmed the “medial-over-lateral advantage” (MOLA – Funk & Brugger, 2008; Lameira et al., 2008; Parsons, 1994; Zapparoli et al., 2014) and the speed/accuracy trade-off for visual hand stimuli (Ionta et al., 2007), further showing that these effects are lower for haptic compared to visual stimuli. It is worth noting that our analysis of RT and accuracy was not separated for palm- and dorsum-view stimuli. Some authors identified the MOLA for the mental rotation of visually-presented palm- but not dorsum-view hands (Bläsing et al., 2013; Rangel et al., 2010; Zapparoli et al., 2014). Our findings suggest that the absence of the MOLA for haptic stimuli may be explained, at least partially, by the merging of dorsum and palm views.

Fig. 7 – Significant main effects of Rotation (and no significant interactions for Modality × Rotation) (Model 2) were observed in the occipital, fusiform, and lingual gyri, as well as in the anterior insula. Specifically, in these regions, activation was higher for rotated compared to unrotated stimuli. (A) The whole-brain analysis showed that activation in the middle occipital gyrus, as well as in the fusiform gyrus showed main effects of Rotation. Warm colors represent the intensity of F-values from a group TFCE analysis. (B) The ROI analyses also identified that the left fusiform gyrus, the left lingual gyrus and the left anterior insula showed main effects of Rotation (predefined ROIs are shown in green). Results for haptic and visual stimuli are shown in red and blue, respectively. Med = medial, Lat = lateral.

Table 6 – Regions with significant main effect of Rotation (and no significant interactions for Modality × Rotation) (Model 1) found in whole-brain analysis (Fig. 7A).

<table>
<thead>
<tr>
<th>Region Label</th>
<th>Extent (mm³)</th>
<th>F-value</th>
<th>MNI Coordinates</th>
<th>TFCE p-value for combined peak-cluster-level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right middle occipital gyrus</td>
<td>2504</td>
<td>3.72</td>
<td>32 -86 18</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Right fusiform gyrus</td>
<td>1408</td>
<td>3.58</td>
<td>28 -66 -8</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>


The effects of Rotation were positive for haptic stimuli but negative for visual stimuli in sensorimotor regions (primary and secondary somatosensory cortices and supramarginal gyrus; Fig. 4). The primary somatosensory cortex processes and encodes somatosensory input, while the secondary somatosensory cortex is involved in high-level haptic processing, including sensorimotor integration (Chen et al., 2008) and body representation (Corradi-Dell’agery, the ability to mentally visualize one’s own hands)

4.2. Differential activation of the sensorimotor network between haptic and visual mental rotation of hands

The rotation-dependent deactivation might have been enhanced in our experiment, since the participants were explicitly asked to explore haptically the half sphere while performing the visual mental rotation of hands. Thus, the haptic input in somatosensory regions was already allocated with stimulus-unrelated load, leading to higher suppression of rotation-related activity. Interestingly, we also observed activation of the somatosensory cortex for any rotation of haptic stimuli, and not modulated by the Rotation per se (Figs. 4 and 5A). This binary switching for haptic stimuli corroborates the idea that the sensorimotor cortex might not contribute to the rotational component, but it might instead be related to the process of body ownership, storing, and reactivation of motor aspects that facilitates the laterality determination (Berneiser et al., 2018).

<table>
<thead>
<tr>
<th>Rotation</th>
<th>Effect size</th>
<th>DoF</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
</table>
| Left fusiform gyrus – main effect of Rotation –
  F(3,90) = 11.8, η² = .28, p < .0001; main effect of Modality – F(1,30) = 37.5, η² = .56, p < .0001
0°—Med                   | –.16        | 90  | –2.80   | .04     |
0°—180°                  | –.33        | 90  | –5.62   | <.0001  |
0°—Lat                   | –.22        | 90  | –3.90   | .0011   |
Med—180°                 | –.17        | 90  | –3.02   | .020    |
Haptic – visual          | –.41        | 30  | –6.12   | <.0001  |
Left lingual gyrus – main effect of Rotation –
  F(3,90) = 6.61, η² = .18, p = .0016; main effect of Modality – F(1,30) = 6.53, η² = .18, p = .026
0°—180°                  | –.31        | 90  | –4.38   | .0002   |
180°—Lat                 | .19         | 90  | 2.73    | .04     |
Haptic – visual          | .26         | 30  | 2.56    | .016    |
Left anterior insula – main effect of Rotation –
  F(3,90) = 5.14, η² = .15, p = .006
0°—180°                  | –.28        | 90  | –3.49   | .005    |
180°—Lat                 | .27         | 90  | 3.30    | .008    |

4.3. Differential activation in occipital, parietal, and frontal regions between haptic and visual mental rotation of hands

Traditionally, mental rotation has been bound to visual imagery, the ability to mentally “visualize” objects’ spatial transformations (Kosslyn et al., 1995; Paschke et al., 2012; Tomasin & Gremese, 2016). However, mental rotation was shown to not be exclusively dependent on visual imagery (Marmor & Zaback, 1976; Toussaint et al., 2012). Specifically, mental rotation of body parts is thought to recruit both motor cognitive strategies (Cooper & Shepard, 1975; Parsons, 1994; Sekiyama, 1982) and visual imagery (Berneiser et al., 2018; de Lange et al., 2006; Zacks et al., 2003). We now discuss that, since haptic exploration of body parts induces stronger motor imagery compared to visual exploration (Kitada et al., 2010; Volcic et al., 2009) and based on the presented brain imaging findings, changing the sensory nature of the stimulus can modulate the relative weighting of motor and visual imagery in mental rotation of hands.

Haptically-based mental rotation was (linearly) associated with activity in the premotor cortex (Figs. 5A and 6A). The premotor cortex, largely found to be involved in mental rotation of hands (Creem et al., 2001; Perruchoud et al., 2016; Vingerhoets et al., 2002; Zapparoli et al., 2014), was also related to motor intention and preparation, necessary for the internal simulation of motor action of rotation of one’s own hands.
Based on the comparisons of activation in the premotor cortex between haptic and visual stimuli shown in Table 4, the higher involvement of the premotor cortex in haptic mental rotation of hands suggests that this task might rely more on the use of motor imagery strategies and on a stronger adoption of a first-person frame of reference compared to visual stimuli (Kitada et al., 2010; Prather & Sathian, 2002).
Furthermore, similar to sensorimotor regions, even low rotations of haptic stimuli were sufficient to activate the premotor cortex, suggesting prompt embodiment of haptic stimuli at any rotation, not observed for visual stimuli. Because the premotor cortex is a hub for sensorimotor integration (Pamplona et al., 2021), it might be acting as a bridge between perceptual haptic input and body ownership, supporting the mental spatial transformation of the embodied hand.

Conversely, visually-based mental rotation was (linearly) associated with activity in the occipital cortex and right intraparietal sulcus (Figs. 5B and 6B). Although these regions are canonically reported to be involved in mental rotation of hands (Ecker et al., 2006; Vingerhoets et al., 2002), their activation depends on the sensory modality of the stimuli. The higher involvement of the parieto-occipital cortex in visual mental rotation of hands suggests a stronger reliance of this task on visual imagery strategies for visual (Ecker et al., 2006; Zacks, 2008) compared to haptic stimuli. The activation of the IPS may be related to its core role in the transformation of visual information using an egocentric coordinate system, location of body part, and updating of representation during imagined movement (Berneiser et al., 2018; Creem et al., 2001; de Lange et al., 2006; Gogos et al., 2010; Kashuk et al., 2017; Vingerhoets et al., 2002; Zacks, 2008). Finally, rotation effects in the SMA (Fig. 5B) for visual stimuli represent the joint component of motor imagery also for the visual modality. In particular, the SMA might have been involved in suppression of movement, since it was only observed for visual stimuli (Tomasino & Greemese, 2016). Taken together, since premotor and occipital cortices are known to be involved in both motor (Hété et al., 2013) and visual imagery (Spagna et al., 2021), respectively, we propose that the modulation of sensory modality in mental rotation shifted the weighting between motor and visual imagery. This postulate is in line with other studies that highlighted the demand for motor strategies in mental rotation depending on several experimental manipulations, such as the comparison between mental rotation of palm-versus dorsum-view hands (Zapparoli et al., 2014), hands versus full-bodies (Perruchoud et al., 2016), as well as the effects of task training (Berneiser et al., 2018).

4.4. Common effects of rotation in brain activity for haptic and visual mental rotation of hands

Neural activity in the left fusiform and the left lingual gyri presented effects of Rotation regardless of the sensory modality of the stimulus (Fig. 7B). In addition, while in the left fusiform gyrus the average activity was higher for visual than haptic mental rotation, activity in the left lingual gyrus was higher for haptic than visual mental rotation. Both fusiform and lingual gyri were previously found to be involved in recognition of body parts (Kitada et al., 2009; Peelen & Downing, 2005). Conversely, the left fusiform gyrus is solidly linked to visual imagery, as argued in a recent meta-analysis study that considers evidence for behavioral outcomes after brain damage (Spagna et al., 2021). Therefore, we suggest that the higher rotation-related activation in the left fusiform gyrus might be evidence for a higher engagement of visual imagery during visually compared to haptically-mediated mental rotation of hands. Interestingly, the lingual gyrus is presumably the core of spatial representation of objects and body parts perceived via haptic exploration and it is particularly sensitive to the mental representation of body parts haptically explored (Kitada et al., 2009). Moreover, tactile tasks, such as Braille reading and object recognition, applied to blind individuals robustly activates the calcarine sulcus (near the lingual gyrus) (Büchel et al., 1998; Tal & Amedi, 2008).

Since also congenitally blind individuals can perform mental rotation (Marmor & Zaback, 1976), they may be creating spatial representations processed in the lingual gyrus that, similar to visual images, have all necessary attributes to enable their spatial transformation. Unlike middle and inferior occipital areas that only get activated with visual stimuli (de Lange et al., 2006 and Fig. 5B), the lingual gyrus shows Rotation effects for both visual and haptic stimuli (de Lange et al., 2006; Prather et al., 2004). The higher rotation-dependent activity in the lingual gyrus for haptic stimuli, combined with the findings of the sensorimotor cortex being activated but not modulated by rotation of haptic stimuli, suggests a two-level neural processing of haptic mental rotation of hands. First, sensorimotor regions act by self-embodying the hand stimulus, thought to facilitate task performance (see next section). Second, we propose that a spatial representation of embodied haptic stimulus is processed or facilitated in the lingual gyrus. Therefore, the left fusiform gyrus and the left lingual gyrus may act on the interplay between visual imagery and spatial transformation after body ownership, respectively.

Finally, common effects of rotation-dependent activation were observed in the anterior insula, regardless of the type of stimuli (Figs. 5A and 7B). The activation of the anterior insula may be related to its involvement in processing of body ownership (Pamplona et al., 2021) and subjective experience (Tsakiris, 2010) during mental rotation of hands.

4.5. Associations of brain activity and RT and implications in motor and visual imagery

Activity in sensorimotor regions was associated with shorter RT for mental rotation of haptically-presented hands (Fig. 7A), while activity of visual areas was associated with longer RT for mental rotation of visually-presented hands (Fig. 7B). Previous studies suggested that the engagement of an internalized motor strategy contributes to a superior performance of the mental rotation of hands, compared to unstructured visual imagery (Berneiser et al., 2018; Vingerhoets et al., 2002). It was also observed that practice leads to both improvement in performance and increased activation in motor-imagery-related areas (Berneiser et al., 2018). Our results indicate that a higher activation of motor-imagery-related areas led to lower difficulty or effort in performing the task for rotated stimuli. Such finding corroborates that a shift from visual to motor imagery was promoted through haptic stimuli. Besides motor imagery, activity in precentral and postcentral gyri indicates that constant updating of the haptic representation also supports fast spatial transformation. Conversely, when a higher activation of visual-imagery-related areas is employed for visual stimuli, the performance is slower, supporting the
concept that this cognitive function might be sub-optimal for the mental rotation of hands. Since we observed a higher negative relationship between visual-imagery activity and performance for the awkward posture, we suggest that the recruitment of visual-imagery areas is preferred over motor-imagery ones for biomechanically-challenging postures.

Interestingly, we also observed that the association between DMN activity and RT was more positive for unrotated compared to rotated visual stimuli. Historically, the DMN was first characterized by its increased activity in passive mental states, such as in baseline conditions during attentional tasks, hence misleadingly referred to as a “task-negative network” (Fox et al., 2005; Spreng, 2012). However, there is convincing evidence that DMN is actively involved in internally-oriented tasks or self-generated thoughts (Andrews-Hanna et al., 2014; Harrison et al., 2008; Mason et al., 2007; Spreng, 2012). As an example, Harrison et al. showed that when individuals were asked to engage in a moral dilemma task, a task that elicits internally oriented mental processes, there was task-related activation in the DMN (Harrison et al., 2008). This way, the DMN presents a dichotomous mechanism that depends on the nature of the task (Spreng, 2012). More specifically, the swaying between activation and deactivation in the DMN reflects the dichotomy between internally- and externally-directed cognition, respectively (Andrews-Hanna et al., 2014). DMN activation has been associated with lower attentional performance and attentional lapses (Mason et al., 2007; Weissman et al., 2006). On the other hand, DMN deactivation represents the suppression of internally-oriented thoughts that can be detrimental to performance in externally-oriented attentional tasks (Mason et al., 2007; Weissman et al., 2006). Importantly, the attentional load during a task is proportional to the strength of DMN deactivation (Kelly et al., 2008). Therefore, a more positive relationship between RT and DMN activity reflects lower suppression of internally-oriented thoughts and worse performance in an externally-oriented attentional task – such as the proposed visual/haptic mental rotation task. Conversely, a more negative relationship between RT and DMN activity reflects better suppression of thoughts irrelevant to the task and better performance. In the present study, we observed that the association between RT and DMN activity was more positive for nonrotated compared to rotated visual stimuli, possibly reflecting that subjects suppressed internal cognitive processes more successfully during trials with higher attentional load (rotated stimuli). We observed no differences across the associations between DMN activity and RT for haptic stimuli, an indicative that an attentional task using haptic stimuli can be less susceptible to the interference of internally-oriented cognition in task performance, probably because more neural resources are necessary during haptic trials.

4.6. Separation of neural engagement and neural effort through modeling trial-by-trial RT

Here, we used a mapping framework that separates brain processes using distinct models: specifying the RT either as a regressor of interest or as a covariate. This way, we reconciled both the differential neural response to conditions of interest and the trial-to-trial variability in RT for fixed levels of Rotation, revealing distinct aspects involved in the same task (Bode et al., 2018; Woolgar et al., 2014). Such dissociation was performed through (1) regressing out the RT from condition-related brain activity and, conversely, (2) verifying the relationship of RT and brain activity. Since the regressors here are colinear (i.e., stimulus and degree of Rotation have the same onset), the stimulus-related activity needs to be properly modeled to avoid misinterpretations (Mumford et al., 2015). On one hand, brain activation can be most informative when independent of RT, associated with neural engagement (Taylor et al., 2014). Hemodynamic responses increase with RT (Domagalik et al., 2014; Yarkoni et al., 2009), therefore differential activations across conditions evidencing different neural mechanisms may be simply a product of differences in duration of stimulus (Taylor et al., 2014). In fact, widely distributed, common activations were observed to be correlated merely to the variance in RT across unrelated tasks (Yarkoni et al., 2009). This observation might actually reflect sustained goal-directed attention until a response is made (Domagalik et al., 2014; Weissman et al., 2006; Yarkoni et al., 2009) and may lead to wrong inferences about neural mechanisms and misinterpretation of results. On the other hand, neural associations can also be related to the required neural effort and processing demands, covarying with RT (Taylor et al., 2014). The RT is a behavioral index of key cognitive processes of interest in psychological tasks and can also index effort or difficulty (Steinborn et al., 2018; Woolgar et al., 2014). RT can be experimentally addressed through event-related designs, more appropriate to isolate neural activity associated with a cognitive function and to control for neural components unrelated to the task, such as visual stimulation (Paschke et al., 2012; Seurinck et al., 2005). Here, by considering distinct cognitive models that regressed in and out RT and by using an event-related design, we investigated different neural processes related to mental rotation of hands.

We endorse the recommendation (Domagalik et al., 2014; Mumford et al., 2012; Woolgar et al., 2014; Yarkoni et al., 2009) that the relationship between RT and conditions of interest in cognitive tasks should be addressed through hypothesized models accounting for the RT.

4.7. Limitations and future directions

First, although the participants were instructed to use the same pattern of stroking to haptically explore both the plastic hands and the half sphere, we cannot rule out stroking differences between the two modalities, which might have affected motor-related components in brain activity. Hand movement associated with stroking differences between sensory modalities could have been, to a certain extent, quantified with an electromyogram (EMG) during the experiment, the gold standard for controlling muscle activity. However, reliable EMG acquisition is complicated by compatibility issues and electromagnetic interference in the MR scanner environment (Hétu et al., 2013). Second, many studies report the involvement of the cerebellum in the task of mental rotation of hands (Berneiser et al., 2018; de Lange et al., 2006; Kashuk et al., 2017; Tomasinò & Gremsen, 2016; Vingerhoets et al., 2002). In our study, cerebellum coverage was dependent on the brain size of the participant and therefore not included in the ROI analysis.
Third, we did not observe MOLA for haptic stimuli, despite previous evidence that it exists for haptic stimuli in the palm and not in the dorsum view (Rangel et al., 2010). MOLA observed only for palm view was also reported for visual stimuli (Zapparoli et al., 2014). In our study, the interaction Modality × Rotation × View was not significant and therefore palm and dorsum views were collapsed in the fMRI analysis. Fourth, besides the association with mental rotation, the activation of IPS can also be partially linked to saccadic eye movement (Levy et al., 2007). In our study, rotation-related effects were more strongly observed in IPS for visual stimuli but might have been confounded by eye movement. An fMRI study that combines mental rotation of haptically- and visually-presented hands and eye-tracking might help clarify this entanglement. Fifth, in our strategy to deal with a non-null number of correct trials for a condition, we applied concatenation of functional task runs, which may also arise potential issues. We accounted for the run effect by constructing regressors of no-interest to represent each run. We also acquired additional volumes (for approximately 20 sec) after the last trial of each run to mitigate effects that could come from convolving the hemodynamic response function with data from the subsequent run.

As future directions, we first mention that a variant of this experiment could be used to investigate differences in the visual field between blind and sighted individuals. We also suggest that the relationship between the sensorimotor and the visual field could be addressed through causality techniques. In addition, comparing right- and left-handers could provide further details about the role of the sensorimotor network in motor imagery. Finally, the evaluation of visuomotor skills through mental rotation of hands is especially useful for several conditions, including traumatic brain injury (Oostra et al., 2012), Parkinson’s disease (Amick et al., 2006), and hemiparetic cerebral palsy (Crajè et al., 2010). The haptic/visual protocol presented here could be used, for instance, to use mental rotation as a screening tool to establish the status of sensory processing in body representation in clinical settings.

5. Conclusions

By modulating the nature of sensory stimuli, we showed that brain areas related to motor and visual areas differed in terms of relative weighting in mental rotation of hands. Haptically-mediated mental rotation of hands evoked an activity pattern more associated with motor imagery compared to visual stimuli. Visually-mediated mental rotation recruited distinct networks that presumably combined both motor and visual imagery. We further showed that, when motor-imagery-related regions are recruited, performance in mental rotation of haptically-presented hands is improved. In contrast, a performance detriment in mental rotation of visually-presented hands is observed when visual-imagery-related regions are recruited. The present findings support that mental rotation of hands presented in different sensory modalities stimuli can be a powerful protocol to evaluate the status of brain responsiveness to body-related multisensory stimulation.
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