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# Mental Rotation Ability: Right or Left Hemisphere Competence? What We Can Learn from Callosotomized and Psychotic Patients

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**Abstract:** Mental rotation is an abstract operation whereby a person imagines rotating an object or a body part to place it in a different position. The ability to perform mental rotation was attributed to right hemisphere for objects, to the left for one's own body images. Mental rotation seems to be basic for imitation in anatomical mode. Previous studies showed that control subjects, callosotomized and psychotic patients chose the mirror-mode when imitating without instructions; when asked to use the same or opposite limb as the model, controls chose the anatomical mode, callosotomized patients mainly used mirror mode, psychotic patients were in between. The preference of callosotomized subjects is likely due to defective mental rotation, because of the lack of the corpus callosum (CC), thus suggesting an asymmetry in the hemispheric competence for mental rotation. Present research investigated the mental rotation ability in control subjects, callosotomized and psychotic patients. All subjects were shown pictures of a model, in first or third person perspective, with a cup in her right or left hand. They had to indicate which model's hand held the cup, by answering with a verbal or motor modality in separate experimental sessions. In both sessions, control subjects produced 99% of correct responses, callosotomy patients 62%, and psychotic patients 91%. The difference was statistically significant, suggesting a role of the CC in the integration of the two hemispheres' asymmetric functions in mental rotation.

**Keywords:** mental rotation; split-brain patients; psychotic patients; imitation; anatomical perspective; corpus callosum

#### 1. Introduction

Mental rotation is an abstract operation whereby a person imagines rotating an object or a body part so as to place it in a different position [1]. It is a form of mental imagery [2], a complex cognitive process having its roots in real perception, through which we recall from memory, generate and manipulate mental representations, in the absence of environmental input [3]. Mental rotation is performed in absence of real movement, and it can take place either in an egocentric or in an object-reference

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frame [4]. In an egocentric reference-frame the visuo-spatial analysis refers to locations of objects from the observer's point of view (i.e., frames locating things up-down, front-back, and left-right with respect to the observer; [5]); in the object-reference frame analysis refers to environmental coordinates (i.e., frames locating things up-down, front-back, and left-right respect to external coordinates; [6]. In object-based mental rotation tasks, the objects must be judged in relation to each other while the relationship between the environment and the observer remains fixed. In egocentric mental rotation tasks, typically involving body-related stimuli, individuals have to imagine themselves rotating in order to complete the task.

Mental rotation was first revealed in behavioral experiments [7,8] by measuring the time to make a judgment about a rotated object: the time often increases in a near-linear fashion with the amount of rotation required to bring the object into alignment with a comparison object or with a previously learned template [9]. This effect has been observed with different kinds of stimuli: both geometric and "abstract", such as letters, lines, polygons and three-dimensional cubes, and embodied and concrete, such as hands, legs, and whole-body figures [10–13].

Several other studies analyzed the relationship of mental rotation ability with development and age. They have shown that the ability to transform mental images is present in very young children, reaches higher levels during adolescence and declines with ageing (see data and literature in [2]). The severity of the decline in mental rotation performance often depends on the stimuli used and the kind of task (object-based vs. egocentric; [14]). It has been shown that mental rotation is facilitated with human figures as stimuli and egocentric tasks, and that males are generally more accurate than females [14]. As regards gender differences in mental rotation, although several studies indicate robust effects generally favoring males [15,16], and agreed that these differences emerge at the age of around 8 years, the question is still matter of debate.

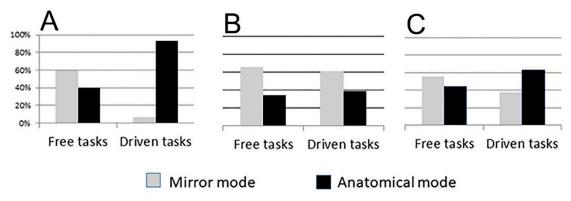
Previous studies, trying to allocate this abstract function in the brain, suggested that mental rotation of objects can belong to the right hemisphere, that of body images to the left, although with less evidence ([9,17,18]. The issue is not solved yet, since many other studies claim against the right hemisphere dominance for objects' mental rotation [1,19]. However, very seldom the mental rotation of the whole body image in a front-back direction was directly assessed [20–22].

Mental rotation is strictly concerned with anatomical imitation, as suggested in previous behavioral studies. The imitation is the earliest form of relationship between individuals and can be considered the simplest form of social behavior. Imitation plays a central role in development, motor learning, communicative competence and acquisition of social skills. Generally, when asked to imitate a model gesturing facing the imitator, one can choose between two imitating strategies: a mirror-mode (specular), i.e., using the right limb to copy a spatially matched left limb gesture of the facing model, or an anatomical-mode, i.e., using the right limb for imitating an anatomically matched right limb gesture by the model. For successful anatomical imitation (3PA and 1PC; [23]), individuals have to make a comparison between the representations of the self and the other; this operation involves a transformation of the egocentric perspective to the allocentric one [24], which requires a mental rotation activity. Therefore, imitation requiring mental rotation can be defined as "anatomical", while "mirror" refers to imitation which occurs without mental rotation [23].

A recent research investigated the imitative behavior in patients with therapeutic corpus callosum (CC) resection and in healthy adults with an intact CC [25,26]. The study analyzed the perspective used by participants in imitating intransitive gestures. It has been shown that all subjects, when executing spontaneous imitation (free task), used the mirror mode (60% controls, 66% callosotomy patients; Figure 1); when instructed to "use the same limb as the model" (driven task), the control group chose the anatomical mode (93%), but the callosotomy patients still preferred the mirror mode (i.e., 39% anatomical mode; Figure 1; [25,26]). Later, an impairment of the anatomical imitative competence has been evidenced also in psychotic patients (41% anatomical imitation in free sessions, 64% in driven sessions; Figure 1; [27]), suggesting that individuals with surgical resection, microstructure alteration (as those reported in schizophrenic patients [28,29]), or incomplete maturation of the CC [30],

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might be unable to execute the mental rotation. It has therefore been hypothesized that the different performances of the two patient groups with respect to the controls could possibly be due to an impaired capacity for mental rotation, in which the corpus callosum (CC) might have a role. The need of the CC seems thus to suggest that anatomical imitation, and therefore mental rotation ability on which anatomical imitation is based, are sustained by neural circuits including cortical areas of both hemispheres with different functions, according to an asymmetric distribution of competences.



**Figure 1.** Responses proportion (%) of imitative perspective in free and driven sessions in control subjects (**A**), callosotomized patients (**B**) and psychotic patients (**C**). **A**, modified from [25]; **B**, from [26]; **C**, from [27].

Since a close correlation between anatomical imitation and mental rotation could be supposed, the present research investigated the ability to perform mental rotation in control subjects, in callosotomized patients and in psychotic patients. The purpose of this study was to test the hypotheses suggestive of a central role of the interhemispheric connections in mental rotation, since it is not clear yet whether this ability resides in the right or left hemisphere, or requires the cooperation of both. Two separate experimental sessions were provided; a verbal and a motor task. In the first, the verbal task, participants were asked to answer by voice whether the hand holding the cup in the displayed picture was the left or right hand. In this task it was possible to evaluate the mental rotation ability through a hand-laterality judgement. In the second, the motor task, participants were asked to indicate whether the hand holding the cup was the left or the right by lifting their own left or right hand. Preliminary results have been presented in abstract form [31].

## 2. Materlials and Methods

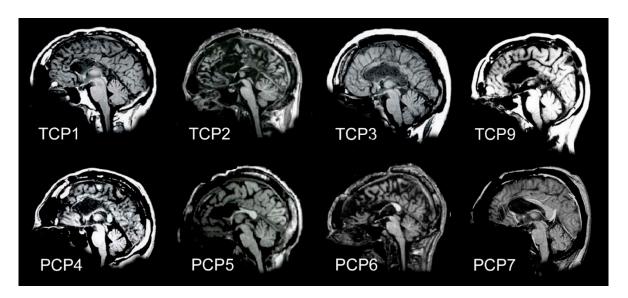
## 2.1. Participants

Forty-five subjects were recruited, grouped according to control subjects, callosotomy patients and psychotic patients. Control subjects were 30 healthy adults (aged 24–69 years, mean age 41.6, SD = 14.3; 17 males; Table 1). Callosotomy patients were 9 right handed epileptic patients (aged 26–57 years, mean age 46.9, SD = 10.2; 5 males; Figure 2; Table 2) who underwent complete or partial surgical resections of the corpus callosum to curb the severity of their seizures, and followed up at the Neurology Clinic of "Umberto I" Hospital, Ancona. Psychotic patients were 6 patients (19–45 years, mean age 34.2, SD = 9.5; 4 males; Table 3) with schizophrenic spectrum disorders, followed up at the Jesi Hospital. The handedness of all subjects was evaluated using the Edinburgh Inventory [32]; all of them had normal or corrected-to-normal visual acuity. The experimental protocol was approved by the Ethics Committee of Università Politecnica delle Marche (Ancona, Italy), and all participants gave their informed consent to the experimental procedure.

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Table 1. Dat	a ot co:	ntrol su	biects.
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Subject	Gender	Age	Oldfield Score
CS1	M	26	10
CS2	F	46	10
CS3	M	48	10
CS4	F	63	30
CS5	M	69	12
CS6	M	26	17
CS7	M	24	12
CS8	F	52	12
CS9	M	61	14
CS10	F	52	14
CS11	M	58	14
CS12	M	60	12
CS13	F	24	14
CS14	F	55	10
CS15	F	50	10
CS16	F	37	10
CS17	M	26	10
CS18	M	59	10
CS19	F	53	10
CS20	F	28	10
CS21	M	29	10
CS22	M	27	10
CS23	M	26	10
CS24	M	42	10
CS25	F	39	10
CS26	F	45	35
CS27	M	25	12
CS28	M	27	12
CS29	F	40	12
CS30	M	31	10



**Figure 2.** MR images of midsagittal brain slices from 8 of 9 patients with total (CP1, CP2, CP3 and CP9), and partial anterior (CP4, CP5, CP6 and CP7). One patient (CP8) was not subjected to MRI because of a metallic arterial clip in her brain.

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Patient	Gender	Age	Oldfield Score	Callosotomy
TCP1	M	49	10 (right)	Total
TCP2	M	39	21 (right)	Total
TCP3	F	37	10 (right)	Total
PCP4	M	45	10 (right)	Partial Anterior
PCP5	F	40	10 (right)	Partial Anterior
PCP6	M	49	10 (right)	Partial Anterior
PCP7	M	55	10 (right)	Partial Anterior
PCP8	F	51	10 (right)	Partial Anterior
TCP9	F	57	10 (right)	Total

**Table 2.** Data of callosotomized patients.

**Table 3.** Data of psychotic patients.

Patient	Gender	Age	Oldfield Score	Diagnosis
PP1	M	33	16 (right)	Schizophrenia
PP2	M	19	10 (right)	Schizophrenia
PP3	F	45	18 (right)	Schizophrenia
PP4	M	28	14 (right)	Schizophrenia
PP5	F	40	10 (right)	Schizophrenia
PP6	M	40	44 (left)	Schizophrenia

Because of the different performance often referred to as totally versus partially callosotomized patients [31], the callosotomy group was split into two, and therefore our study was conducted on four groups of people. Hereafter, the four groups will be reported as Control Subjects (CS), Partially Callosotomized Patients (PCP), Totally Callosotomized Patients (TCP), and Psychotic Patients (PP).

## 2.2. Stimuli

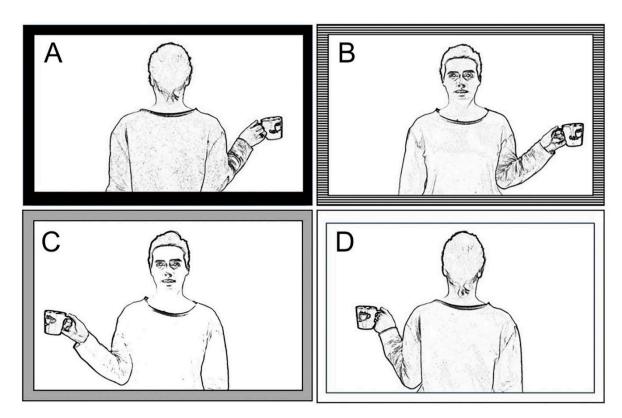
Stimuli consisted of pictures of a model, in a 1st or 3rd person perspective (at 0° and 180°), holding a cup either in her right or left hand (4 combinations; Figure 2).

#### 2.3. Design and Procedure

All subjects underwent to a behavioral stimulation protocol showing a human static model holding a cup in her right or left hand; the images were shown to participants in a 1-s presentation on a pc screen, in the central visual field, in 1st and 3rd person perspectives (at 0° and 180°), and in random order in the working session. All subjects were asked to indicate in which model's hand the cup was being held. They were asked to use, in two separate sessions, a verbal or a motor response modality: in the verbal modality they had to pronounce the words "right" or "left"; in the motor modality they had to lift their right or left arm, according to the model's hand in which the cup was hold, in their judice.

Each protocol included two sessions, one verbal and one motor. Each session was composed by 4 pictures showing a model alternatively in 1st person perspective with the cup in her right hand (Figure 3A); in 3rd person perspective with the cup in her left hand (Figure 3B); in 3rd person perspective with the cup in her right hand (Figure 3C); or in 1st person perspective with the cup in her left hand (Figure 3D). The 4 different images were presented 12 times each, for a total of 48 stimuli per session. In total each subject/patient was shown 96 pictures, 48 during the verbal session, 48 (the same) during the motor session.

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**Figure 3.** Images composing the behavioral protocol to evaluate the ability to perform mental rotation. (**A**), Model shown in 1st person perspective with the cup in her right hand; (**B**), model in 3rd person perspective with the cup in her left hand; (**C**), model in 3rd person perspective with the cup in her right hand; (**D**), model in 1st person perspective with the cup in her left hand.

Responses were registered by the investigator. The same behavioral protocol was presented to the callosotomy patients and psychotic patients. The results have been analyzed in terms of statistically significant evidence, and the possible influence of confounding factors (i.e., gender, handedness, and others; see below) will be assessed.

To provide a correct response to frames A and D, a mental rotation operation is not required, whereas to respond correctly to frames B and C does require mental rotation. Performances were evaluated by counting the correct responses in each session.

### 2.4. Statistical Analysis

A preliminary analysis was conducted separately for each group (controls, callosotomized and psychotic patient). For each patient group the proportion of correct answers was calculated.

The statistical analysis was then carried out to evaluate how the variable of interest, N, could be modified by different confounds. The response variable of interest, N, was the number of correct answer for each set of repetitions. N is an ordinal variable which assumes all integer values from 1 to 12. The following factors, considered as possible explanatory confounding variables, were considered in the statistical analysis:

**Age**: the age of the individual;

Gender: an indicator variable that was assigned the value of "M" for males and "F" for females;

Oldf: Oldfield classes (0 if Oldfield is less than or equal 30 and 1 otherwise);

**St**: session type (Verbal = 1; Motor = 0);

**Mp**: model position (Third person = 0; First person = 1);

**Cp**: cup position in the model's hand (Right hand = 0; Left hand = 1);

**Pat**: presence and kind of pathology (healthy controls = 0; psychotic patients = 1; partially callosotomy patients = 2; totally callosotomy patients = 3).

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We coded the four categories of Pat with three dummies variables, Pat1, Pat2 and Pat3, as follows:

$$Patj = \begin{cases} 1 \text{ if } Pat = j \\ 0 \text{ otherwise} \end{cases} \text{ for } j = 1, 2, 3.$$

Individuals of the control group were assigned a 0 on all the three dummy variables.

Concerning the Oldfield score, the scale we used to test the patients' handedness, the possible values range from 10, completely right-handed subject, to 50, completely left-handed subject. To simplify the analysis, by transforming this continuous variable into a binary one, we choose to consider right-handed subjects as those reporting an Oldfield score from 10 up to 30, and left-handed subjects reporting a score >30 up to 50.

The selection strategy adopted to identify the factors that need to be included in an appropriate statistical analysis is reported in [33]. Analysis of the data and the respective diagrams was carried out with the R statistical program [34] and Microsoft Excel<sup>®</sup>.

Considering that N, the number of correct responses, is an ordinal variable, we fitted our data using a cumulative link mixed model:

$$logit(P(N_i \le k)) = \theta_k - \mu(Gender_i, Age_i, OldCl_i, St_i, Mp_i, Cp_i, Pat1_i, Pat2_i, Pat3_i) - u(s_i)$$
 (1)

where  $i=1,\ldots,n=45$ ; index all the individuals and  $k=0,\ldots,K=12$ ; index the number of correct answers. This is a model to relate the cumulative probability that the i-th individual gives the number of correct answers less or equal to k,  $\{N_i \le k\}$ , with the considered explanatory variables. The parameters,  $\{\theta_k\}$ , are known as threshold parameters or cut-points. We take the individual effects,  $u(s_i)$ , to be random, and assume that they are independent, normally distributed with zero mean and variance  $\sigma^2$ .

Finally, we suppose that  $\mu(Gender_i, Age_i, OldCl_i, St_i, Mp_i, Cp_i, Pat1_i, Pat2_i, Pat3_i)$  is a linear combination of the values of the explanatory variables:

$$\mu = b_1 \cdot Gender_i + b_2 \cdot Age_i + b_3 \cdot OldCl_i + b_4 \cdot St_i + b_5 \cdot Mp_i + b_6 \cdot Cp_i + b_7 \cdot Pat1_i + b_8 \cdot Pat2_i + b_9 \cdot Pat3_i$$
 (2)

where  $b_i$ , i = 1, ..., 9 are the model parameters.

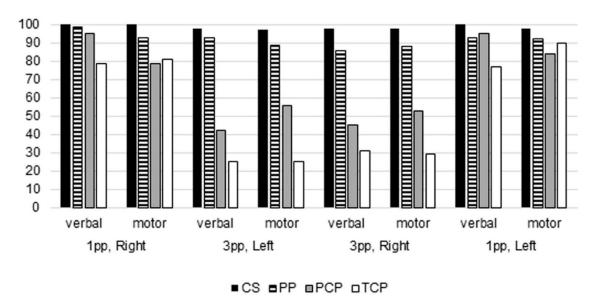
#### 3. Results

The four groups' (CS, PCP, TCP and PP) performances were analyzed in relation to variables belonging to the experimental protocol (position of the model, Mp; position of the cup, Cp) and to variables belonging to the subjects themselves (gender, age, handedness, extent of callosal resection, psychotic pathology). The initial dataset consisted of 2880 observations from 30 CS, 864 observations from 9 CP (480 from PCP and 384 from TCP), and 576 observations from 6 PP, collected during verbal (vs) and motor sessions (ms; 48 per session).

Tasks and Related Results

In both sessions, control subjects produced 99% correct responses (2851/2880), callosotomized patients 62% (537/864), and psychotic patients 91% (524/576). The most striking evidence concerns the different performance when the stimulus was in third person. The difference was more evident in PCP and TCP, less in PP. No difference was appreciable in CS. By analyzing in more details the performances of the different groups, the main difference was observed in the third person presentations, particularly for both groups of callosotomized patients (Figure 4).

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**Figure 4.** Performance of control subjects (black bars), psychotic patients (dashed bars), partially callosotomized patients (gray bars) and totally callosotomized patients (white bars), in verbal and motor sessions, in first and third person presentation, shown as mean percentage values, as a function of the position of the model. When the model was presented in the first person perspective, fewer errors were made by patients. Callosotomized patients' performance was lower when the model was in the third person perspective. CS, control subjects; PP, psychotic patients; PCP, partially callosotomized patients; TCP, totally callosotomized patients; 1pp, first person presentation; 3pp, third person presentation.

By inserting in the model (1) with the linear component (2), all variables potentially influencing the response, i.e., Age, Gender, Oldf, St, Mp, Cp, Pat1, Pat2, Pat3, fitted the model of the data.

The maximum likelihood estimates of the parameters  $b_1$ , ...,  $b_7$ ,  $b_8$ ,  $b_9$ , and of the standard deviation,  $\sigma$ , of the random effects are reported in Table 4.

**Table 4.** Parameter estimates and standard errors of the estimates for the multivariable model for population including control subjects (CS), psychotic patients (PS), partially callosotomized patients (PCP) and totally callosotomized patients (TCP).

Parameter	Estimate	Std. Error	z Value	<i>p</i> -Value
Fixed effects				
$b_1$	0.176	0.490	0.359	0.720
$b_2$	-0.033	0.021	-1.546	0.122
$b_3$	0.623	0.940	0.663	0.507
$b_4$	0.410	0.279	1.470	0.142
$b_5$	1.698	0.318	5.340	< 0.001
$b_6$	-0.308	0.276	-1.117	0.264
$b_7$	-2.183	0.723	-3.020	0.003
$b_8$	-3.800	0.750	-5.064	< 0.001
$b_9$	-5.275	0.811	-6.506	< 0.001
Random effects				
Std.dev.	1.167			

Table 4 shows that only variables Mp (coefficient  $b_5$ ) and Pat (coefficients  $b_7$ ,  $b_8$ ,  $b_9$ ) are significantly associated to the number of correct responses. The model has been therefore reformulated by including only the significant covariates, as follows:

$$\mu = b_1 \cdot Mp_i + b_2 \cdot Pat1_i + b_3 \cdot Pat2_i + b_4 \cdot Pat3_i$$

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The parameter estimates for the new model were reported in Table 5. The coefficients for Patj, j = 1, 2, 3, are all negative and decreasing from  $b_2$  to  $b_4$ , indicating that the increase in the severity of the pathology, from Pat1 to Pat3, significant decreases the probability of correct answers. Actually, psychotic patients (coefficient  $b_2$ , Pat1) performed significantly worse than control subjects, partially callosotomized patients (coefficient  $b_3$ , Pat2) even worse, and totally callosotomized patients (coefficient  $b_4$ , Pat3) represented the group with the worst performance. Conversely, the coefficient for Mp points out that the position of the model in first person perspective increased the probability of correct answer.

**Table 5.** Parameter estimates and standard errors of the estimates for the model including only the variables, model position (Mp) and presence and kind of pathology (Pat), significantly associated to N<sub>i</sub>.

Parameter	Estimate	Std. Error	z Value	<i>p-</i> Value
Fixed effects				
$b_1  \mathrm{Mp}$	1.673	0.314	5.321	< 0.001
b <sub>2</sub> Pat1	-1.923	0.671	-2.864	0.0042
b <sub>3</sub> Pat2	-3.801	0.733	-5.186	< 0.001
b <sub>4</sub> Pat3	-5.231	0.801	-6.528	< 0.001
Random effects				
Std.dev.	1.164			

These results were also evident, although without any statistical validation, in the first level of analysis (Figure 4).

#### 4. Discussion

The present research investigated the ability to perform mental rotation of body images in control subjects, callosotomized and psychotic patients. The choice to study the above mentioned two groups of patient was guided by the following reasons: 1. as previously reported, both callosotomized [26] and psychotic patients [35] showed an impaired ability, more severe in the first group, for anatomical imitation, which likely requires the abstract operation of mental rotation; 2. recent papers reported a partially impaired performance in mental rotation of letters and hand pictures in schizophrenic patients [36,37]. Since both kinds of patients are likely to display a reduction (more severe in the first group) of interhemispheric transfer, due either to interruption of callosal fibers (callosotomized patients), or to microstructural alterations of them (psychotic patients [28,29]), the expected results were therefore to observe a reduced mental rotation ability of body images in both groups of patients, more pronounced in callosotomy ones. Actually, present data demonstrated that control subjects performed the task almost perfectly, in verbal and motor sessions, both when the model was in first-person perspective, and when she was in third-person perspective. Callosotomized patients showed some impairment, mainly in the verbal session and when the model was in third person perspective; psychotic patients too showed an impairment, although less pronounced than callosotomized ones. The present study indicated the central role of interhemispheric connections in mental rotation, and therefore, because of the need of the cooperation of both hemispheres to be performed, strongly suggest the value of considering mental rotation as an asymmetric function.

The statistical analysis demonstrated that the variable mostly influencing the subjects' performance was the position of the model: when she was in third person perspective, both groups of patients displayed a higher proportion of incorrect responses, although psychotic patients performed slightly better than callosotomized patients.

The other variable influencing the performance was the presence of a callosal pathology: partial or total callosal resection, or microstructural callosal alteration likely present in psychotic patients. Actually, the performance obtained by psychotic patients was less poor than that of callosotomized patients, although it was still significantly lower than that of control subjects (Table 3). A difference

could be appreciated also between totally and partially callosotomized patients; however, the very low number of cases prevented an evaluation of the statistical significance.

No differences were observed in the present study depending on age, although the subjects were all adult, nor between women and men, in all groups. No differences were observed due to the position of the cup in the model's hand (right or left), nor could any significant difference be appreciated due to the kind of session, whether verbal or motor.

The present results seem to indicate a role of the corpus callosum in the ability to perform the mental rotation, at least of the whole body image, in that the commissure is lacking in callosotomized patients, and likely impaired in psychotic patients. Further studies, verifying the functional integrity of the corpus callosum in psychotic patients could at least partially answer the question.

The present study analyzes an egocentric transformation task, requiring participants to indicate whether the model's hand holding a cup is a right or a left hand; to answer, the participants have to look at a visual stimulus, a half body human picture presented in back or front perspective (0° or 180°). Behavioral results demonstrated that the orientation of the stimulus (front *versus* back position, i.e., third versus first person perspective) significantly influences the response correctness, mainly in callostomized patients.

The hypothesis advanced in the present work stays for the close correlation between stimulus orientation, mechanisms involved in processing the stimulus (i.e., visuo-spatial match versus mental rotation) and effect that an altered interhemispheric communication could exert onto the performance when the stimulus to be judged is placed in front of the observer, i.e., in third person perspective. As such, because of deficiency in interemispheric communication, callosotomized patients were unable to correctly respond to the task when the stimulus was in front-orientation, because of a failure of the neural circuit involved in mental rotation. It can be suggested, therefore, that mental rotation neural circuit is distributed in both hemispheres.

Many studies have been produced which analyze the egocentric transformation of the whole body. Some of them could be compared with ours, which is also based on an egocentric transformation of the whole body, in particular those describing experimental protocols similar to ours [21,22,38–41]. All of them reported as easier the task of mental rotation of body images, with the performance depending on the disparity angle, i.e., better responses for back (first person) presentation, worst for front (third person).

Parsons [21] examined two related phenomena: the judgment of whether a human body part belongs to the left or right half of the body and the imagined spatial transformation of one's body: observers made left-right judgments of a part of a body whose orientation differed from their own by a rotation about one of 13 axes. To do so, they imagined themselves passing to the orientation of the stimulus. Time for left-right judgments and accompanying imagined spatial transformations depended on the extent of the orientation difference between the observer and stimulus.

Thirioux and collegues [38] investigated the behavioral and neural mechanisms of embodied and disembodied self-location in spontaneous interaction of healthy subjects with an avatar, where participants were instructed to observe the tightrope walker in front and back positions, and to lean when she was leaning (i.e., an imitation task-related). Embodied self-location was the condition in which the subject imagined their own body at the actual body position, and the reproduction of the avatar tilting occurred as in front of a mirror, adopting a visuo-spatial match. Disembodied self-location was the condition in which the imitator was imagining themself at the target body position, by performing a mental rotation of his/her body. The paradigm of that research [38], in which the reproduction of a model's movements occurred in two conditions, first (back position) and third (front position) perspective, could be considered similar to that used in the present study, and the results are comparable. Behavioral results reported correct performances in both tasks requiring embodied or disembodied self-location, and a significant tendency to use disembodied self-location in the spontaneous task. Interestingly, the higher percentage of correct performances was correlated with spontaneous and disembodied self-location performances in response to the stimulus in the back

orientation, and reaction times increased when the rotation angle between the participant and the avatar increased.

In the study of Crescentini and coworkers [22], an "own body transformation" paradigm and a letter transformation task were employed in a group of children ranging from 7 to 11 years of age to investigate the development of egocentric perspective transformations and object-related transformations. A control group of young adults was also administered the two experimental tasks. The results from this latter group for egocentric perspective transformations was similar to those of the present study, by showing that the reaction time was lower and the accuracy was higher for back (first person) presentation. In addition, they found that egocentric perspective transformations develop later than object-based transformations, namely, from 8 rather than 7 years of age. These findings were held to support the view that the two mental spatial transformation systems are separated in that they follow two different developmental trajectories.

Other studies [40] investigated developmental changes in mental rotation performance with a focus on two types of strategies: object-based and egocentric transformations. This study revealed two important findings: 1. an age-related decline in processing speed and the possible role of white matter functionality in mental rotation performance; 2. the observation that children and older adults seem to show deficits in perspective-taking compared to adults. Therefore, they propose that perspective transformations are more sensitive to developmental change compared to object-based transformations.

Jansen and coworkers [41] investigated gender differences in performance and neuronal activity in a mental rotation task with abstract and embodied figures. Participants (26 females and 32 males) completed a chronometric mental rotation task with cube figures, human figures, and body postures. The results were straightforward: depending on angular disparity, participants had a faster reaction time and a higher accuracy rate for embodied stimuli compared to cube figures. They also recorded electroencephalogram (EEG) activity pattern, and showed alterations at the late time interval, even though there were no gender differences in the behavioral data. Thus, the disparate results regarding sex differences that depend on the type of analysis (behavioral versus neurophysiological) should be more thoroughly investigated.

The behavioral data just described all agree in the observation that, concerning egocentric transformation, back orientation produces better performances than front orientation. The difference increases in childhood and senior age (both periods of life in which alterations of the cerebral white matter could be observed), in children because of a still incomplete development, and in older people because of an initial white matter decline. The results of the present study, which reports correct performances in first person perspective ("back orientation") for all participants (controls, callosotomized and psychotics), and reduced performances in psychotic and callosotomized patients, in whom the callosal white matter is damaged, are in line with previous studies.

None of the behavioral studies above mentioned, however, addressed the issue of asymmetric cerebral competence for mental rotation. This notion, strongly suggested by the results of the present research, came out in functional studies, reviewed by Zacks [9], and later by Tomasino and Gremese [40], through an activation likelihood estimation (ALE) meta-analysis. Some observations, suggesting a cerebral specialization for mental rotation, also appeared in previous studies ([18,20,38].

In his review and meta-analysis of neuroimaging studies [9] Zacks posed the research question addressing to whether mental rotation relies on analog spatial representations or on motor simulation. The results of the meta-analysis conducted on 32 neuroimaging studies highlighted a total of 320 activation foci responsive to mental rotation tasks, and included the superior parietal, frontal, and inferotemporal cortex. Most of these brain regions were activated bilaterally, except for the parietal cortex, whose activity was somewhat more consistently observed in the right hemisphere, and the frontal cortex, whose activity was more consistently observed in the left hemisphere [9].

Tomasino and Gremese [42] selected 171 fMRI and PET experiments that investigated mental rotation processes, suggesting a different modulation of mental rotation networks respect the type of stimulus and strategy use to perform the task (motor imagery based versus visuo-spatial imagery).

Studies included in motor imagery mental rotation tasks conteined explicit instructions requiring participants to imagine one's movements or change the body position in space; in studies included in visuo-spatial mental rotation task, participants were explicitly required to imagine the stimulus rotating in the space (e.g., in looking at stimuli pair, choosing if they are identical or mirror or imagining that the table rotated while participant remained stationary; allocentric frame). A further distinction was made within the motor-imagery based mental rotation strategies, between pure motor-imagery (e.g., imagining to rotate one's own arm until this reached the position depicted in the screen) and egocentric mental rotation (e.g., updated the position of an external object after having performed an imagined self-rotation to a new position). In both conditions, a mental rotation of stimuli was requested.

Comparison between motor-imagery-based and egocentric-based mental rotation revealed activations of the left superior parietal lobule, the right postcentral gyrus, the precentral gyrus/middle and superior frontal gyrus bilaterally, and the left inferior occipital gyrus; the inverse analysis activated the left cuneus, the left middle temporal gyrus, the left lingual gyrus and calcarine sulcus, and the right cerebellum.

In the above mentioned study [38], event-related potentials (EPs) were calculated from continuous EEG acquired during the task. EPs mapping revealed different stable brain microstates underlying the spontaneous and disembodied-self-location tasks and the embodied self-location task, suggesting the recruitment of different neural generators. Specifically, in the first two conditions, the involvement of the temporo-parietal junction bilaterally, with a right predominant activation, was observed; also, the posterior parietal cortex and the intraparietal sulcus were activated bilaterally, more prominently in the left hemisphere. During the embodied self-location task, more activated regions were observed in the right hemisphere: the inferior occipital cortex, the postcentral gyrus, the premotor cortex, the dorsolateral prefrontal cortex, the anterior temporal cortex and weaker activation in the temporo-parietal junction. In addition, EP data also showed that brain activations during spontaneous and explicit disembodied self-transformations started earlier for the back than for the front orientation. This could suggest higher difficulty for body transformation in front of a front-oriented stimulus. Summarizing, these data seem to support a prevalent leftward asymmetry in the cortical activation for disembodied self-location, corresponding to the mental rotation for a third person model's presentation of our research, and a rightward asymmetry for the embodied self-location task (i.e., mirror mode, visuo-spatial match).

Participants in the present behavioral study had to produce two different types of response to the same task; in the verbal modality, they observed the target stimulus and reported by voice to the experimenter in which hand (left or right) the model held the cup; in the motor modality, the subjects must raise the hand corresponding to that of the model which held the cup. With respect to type of stimuli, both tasks are laterality judgement like, since target stimuli were body images, presented in first or third perspective, holding a cup in either right or left hand. Therefore, both tasks are supposed to recruit mental rotation when responding to front-facing stimuli, even if through different procedural response-modes (verbal plus motor).

By analyzing previous functional studies [9,38,42], despite the diversity of the investigation approaches (fMRI, EP), and the variables investigated (e.g., instructions, type of stimuli, theoretical definitions), it is possible to identify a common trend of scientific evidences correlating mental rotation to a sort of hemispheric specialization. Specifically, a left lateralization for the parietal cortex and a right specialization for the frontal regions. In an attempt to find likeness between these studies [38,42], a certain factor of concordance can be observed in identifying lateralized activations in motor, sensorimotor and parietal regions during mental rotation. Specifically, the parietal lobe seems to be leftward lateralized, while precentral and postcentral regions appear to be rightward lateralized.

The present paper demonstrates that people with partial or total callosal resection, or with callosal alterations like those reported in schizophrenia, display reduced performance in laterality testing with stimuli in third-person orientation, suggesting an alteration of mental rotation mechanisms, likely due to a defective interhemispheric communication. These results are in line with previous studies

reporting different activations of cortical areas in the two hemispheres, indicating the need for an interhemispheric cooperation, and therefore for an interhemispheric transfer. Present results are also on line with previous indirect evidence suggesting callosal involvement, such as the reduced mental rotation ability of children and old people, likely due to an incomplete callosal maturation and to an initial callosal degeneration, respectively. In conclusion, the present study provides further support to the notion that the mental rotation of body images does require interhemispheric communication, thus leading to the notion of an asymmetric competence.

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