

Cerebellar Contribution to Mental Rotation: a cTBS Study

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Abstract A cerebellar role in spatial information processing has been advanced even in the absence of physical manipulation, as occurring in mental rotation. The present study was aimed at investigating the specific involvement of left and right cerebellar hemispheres in two tasks of mental rotation. We used continuous theta burst stimulation to downregulate cerebellar hemisphere excitability in healthy adult subjects performing two mental rotation tasks: an Embodied Mental Rotation (EMR) task, entailing an egocentric strategy, and an Abstract Mental Rotation (AMR) task entailing an allocentric strategy. Following downregulation of left cerebellar hemisphere, reaction times were slower in comparison to sham stimulation in both EMR and AMR tasks. Conversely, identical reaction times were obtained in both tasks following right cerebellar hemisphere and sham stimulations. No effect of cerebellar stimulation side was found on response accuracy. The present findings document

a specialization of the left cerebellar hemisphere in mental rotation regardless of the kind of stimulus to be rotated.

Keywords Cerebellum · Mental rotation · cTBS · Allocentric–egocentric strategy

Introduction

Mental rotation (MR) is the ability to rotate mental representations of objects [1]. A previous study indicated that there are two distinct ways to mentally rotate an object depending on the implication of motor processes [1]. One strategy of mental rotation, here defined as “egocentric,” is based on the ability to mentally simulate spatial transformation in embodied point of view as if real movements moved the body parts. The second strategy, here defined as “allocentric,” concerns the skill to mentally rotate the stimulus in visual space as if the “object” was shifted by external inanimate forces [2]. Subjects can voluntarily adopt the egocentric and allocentric strategy by request [1], but also in free-choice paradigms, the chosen strategy appears to be triggered by specific stimuli [2]. Although a recent study reported that egocentric strategy may be spontaneously preferred in the mental rotation of abstract figures by subjects experts in motor activities as wrestlers, in naïve subjects, body images tend to trigger an egocentric strategy while abstract figures an allocentric one [3]. While the egocentric strategy can be elicited by body stimuli or by objects to be grasped [4], the allocentric strategy can be elicited by abstract objects without affordance properties [2]. Transcranial magnetic stimulation studies showed that the motor processes are differently involved in relation to the kind of stimulus to be mentally rotated. Increased reaction times (RTs) were recorded when single-pulse transcranial magnetic stimulation (TMS) was applied to the cortical motor area of participants that mentally rotated hand but not letter stimuli [5, 6].

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Cerebellar role in mental rotation functions has been advanced [7]. It remains to be clarified whether the cerebellum is equally involved in egocentric and allocentric MR and whether there is a cerebellar hemispheric specialization for the two types of rotation [7]. Continuous theta burst stimulation (cTBS) was applied on the left or right cerebellar hemisphere in healthy subjects before they performed an Embodied Mental Rotation (EMR) or an Abstract Mental Rotation (AMR) computerized tasks.

Materials and Methods

Participants

A sample of 42 neurologically intact subjects [18 males (42.8 %); mean age \pm SD=28.2 \pm 3.9 years; range 19–35; schooling>13 years] was recruited from universities and hospital personnel by local advertisement. All participants were right-handed as assessed with the Edinburgh Handedness Inventory [8]. Subjects reported normal- or corrected-to-normal vision. The study was approved by the Local Ethics Committee of the IRCCS “Santa Lucia” Foundation and written consent was obtained from all participants after a full explanation of the procedures of the study.

Mental Rotation Tasks

Participants were tested in a quiet room of our lab. They sat comfortably on an armchair at a distance of about 80 cm from a computer monitor; the center was aligned with the subject’s eyes. Computerized versions of the two different MR tasks were used.

To obtain comparable basal mental rotation performances, all subjects underwent a training phase in both MR tasks and

all participants entered the test phase only when they reached a minimum of 80 % of correct responses in the practice phase. Before practice phase, participants read on the computer screen a standardized explanation of the task accompanied by visual examples. They were asked to place their right index finger on one of two central keys of a compatible button box located on their legs, which recorded RTs with 1-ms accuracy. Participants answered “right/same” by pressing the button on the right and “left/different” by pressing the button on the left.

EMR task is a modified version of the Ratcliff’s Little Man [9] programmed to run on computer. The Ratcliff’s Little Man test presents images of a schematic drawing of a human body seen from different orientations (at angles of 0°, 90° to the right, 90° to the left, 180°) in frontal or back views (F or B) in an equal number of trials. The EMR task requires identifying which hand (right or left) was marked in red or blue depending on the stimulus dot presented in the lower portion of the figure (Fig. 1a). The number of right and left dots was balanced across trials.

For the practice phase, we selected eight pictures balanced according to the above-described criterion. Each figure was presented four times in a randomized order, for a total of 32 trials.

In the test phase, we used all the 32 images, eight of these had already been presented in the practice phase. Each of the 32 images was repeated four times, for a total of 128 trials presented in a randomized order. The task was programmed and run by using PsyScope for Macintosh. In both practice and test phases, before the presentation of each image, subject’s attention was invoked to a fixation point indicated by a central black cross remaining on the blank screen for 600 ms. The image of little man, which followed the 400-ms presentation of the blank screen, remained on the screen for 1,500 ms at the end of which the blank screen was again displayed for a maximum of 4,000 ms or until a key

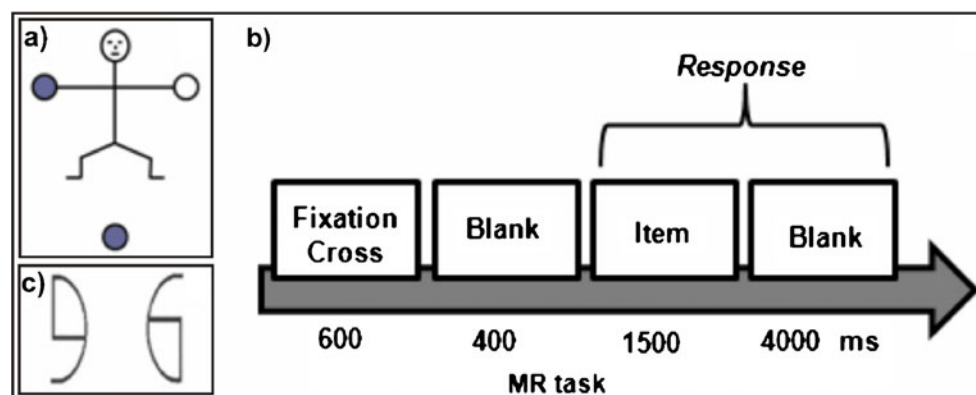


Fig. 1 **a** EMR stimulus example. The red dot actually shown to the participants is depicted as *white* and the blue one as *gray*. The correct response to the item is “right.” **b** Task timing in milliseconds. In both MR tasks, for each trial, the 600-ms presentation of a fixation cross and of a 400-ms blank screen preceded the item presentation during

1,500 ms at the end of which the blank screen was again displayed for a maximum of 4,000 ms or until a key pressing. Only responses given during image presentation or the subsequent blank screen were considered as valid and recorded. **c** AMR stimulus example. The correct response to the present item is “same”

pressing. Then, the fixation point reappeared and the next trial began. Subjects answered “right” or “left” according to which hand they retained to be marked by the stimulus dot. Only responses given during image presentation or the subsequent 4,000 ms (blank screen) were considered as valid and recorded (Fig. 1b).

Parameters considered were as follows: RTs, the time interval between image presentation and key pressing; accuracy, number of correct responses; and angular disparity index, the RTs of the trials when the little man was presented in its prototypical orientation (0°) or rotated away from it (90° to the right, 90° to the left, 180°) and looked in frontal or back views (F or B).

AMR task is a modified version of Thurstone’s primary mental ability test cards [10] programmed to run on computer. The task required to provide the answer “same/different” at the presentation of pairs of similar two-dimensional abstract figures differently rotated from each other. The pairs of images were made up of four different abstract figures (Fig. 1c). The subject had to respond “same” if he/she retained that the two images were overlapping by performing an operation of mental rotation on the plan or “different” if the two images were mirrored. Figures were balanced so that the each pair of images was displayed exactly one quarter of the total times and the correct answer was “same” or “different” in an equal number of trials.

For the practice phase, we selected eight pairs of the four figures each of them was presented four times in a randomized order for a total of 32 pictures.

For the test phase, we used all the 98 images with the repetition of some of them to reach a total of 128 items presented in a randomized order. AMR test was programmed and played by using PsyScope on a Macintosh computer. Times, method, and parameters were those described for the EMR task, with the only difference that in AMR task participants provided the answer same or different rather than right or left and that for this task Angular Disparity Index was not calculated.

TMS Procedure

A MagStim Super Rapid magnetic stimulator (Magstim Company, Whitland, Wales, UK) connected with a figure-of-eight coil with a diameter of 90 mm was used to deliver TBS over the scalp site corresponding to the lateral cerebellum. The magnetic stimulus had a biphasic waveform with a pulse width of about 300 μ s. Three-pulse bursts at 50 Hz repeated every 200 ms for 40 s (equivalent to cTBS) were delivered at 80 % of the active motor threshold (AMT) over the left lateral cerebellum (600 pulses). AMT was tested over the motor cortex of the right hemisphere. AMT was defined as the lowest intensity that produced MEPs of >200 μ V in at least five out of ten trials when the subject made a 10 % of maximum contraction using visual feedback

[11]. The inhibitory effect of cTBS with these characteristics is supposed to last about 60 min [12]. TMS was applied over the left lateral cerebellum using the same scalp coordinates (1 cm inferior and 3 cm left to theinion) adopted in previous studies, in which MRI reconstruction and neuronavigation systems showed that cerebellar TMS in this site predominantly target the posterior and superior lobules of the lateral cerebellum [13, 14]. Although cerebellar stimulation has been originally performed with a double cone coil [15], we used the figure-of-eight coil, since this approach has been adopted in previous investigations in which cerebellar rTMS was shown to be effective in modulating the excitability of the contralateral motor cortex [16, 17]. The coil was positioned tangentially to the scalp, with the handle pointing superiorly. This orientation is able to modulate contralateral M1 excitability [16] and to interfere with cognitive functions such as procedural learning and sub-second time perception when a 1-Hz rTMS paradigm is adopted [14, 18, 19]. For sham cTBS, the coil was positioned on the middle line approximately corresponding to vermian surface but angled away so that no current was induced in the brain. At the end of stimulations, we asked the participants whether they felt some dizziness, vertigo, or gastric discomfort. No participant reported any vestibular symptomatology.

Procedure

Experiment 1 (EMR Task) Twenty-one subjects [nine males (42.8 %)] were randomly assigned to one of the three experimental groups, each of them encompassed seven subjects submitted to EMR task: right cTBS group, in which the subjects performed the EMR task following cTBS over the right cerebellar hemisphere; left cTBS group, in which the subjects performed the EMR task following cTBS over the left cerebellar hemisphere; and sham group, in which the subjects performed the EMR task following sham cTBS.

Experiment 2 (AMR Task) Twenty-one subjects [nine males (42.8 %)] were randomly assigned to one of the three experimental groups each of them encompassed seven subjects submitted to the AMR task: right cTBS group, in which the subjects performed the AMR task following cTBS over the right cerebellar hemisphere; left cTBS group, in which the subjects performed the AMR task following cTBS over the left cerebellar hemisphere; and sham group, in which the subjects performed the AMR task following sham cTBS.

Statistical Analyses

Two-way ANOVAs separately for RTs and accuracy scores, with stimulation (sham \times left cTBS \times right cTBS) and task (EMR vs. AMR) as between-subjects factors were performed.

Angular Disparity Index was calculated by a three-way ANOVA on RTs with stimulation (sham \times left cTBS \times right cTBS) as between-subject factor and view (frontal vs. back) and angle (0° , 90° to the right, 90° to the left, 180°) of the EMR little man as within-subject factors. Post hoc Tukey's tests were performed when required. Effect size was indicated as partial eta square.

The threshold of significance was set at $p < 0.05$.

Experiment 1 and experiment 2 groups (Table 1) were compared for age of participants, and no age difference among groups was found [one-way ANOVA: $F_{5, 36} = 0.37$, $p = 0.87$].

Results

Two-way ANOVA on RTs revealed significant stimulation [$F_{2, 36} = 19.20$, $p < 0.001$, $\eta^2_p = 0.516$] and task [$F_{1, 36} = 60.53$, $p < 0.001$, $\eta^2_p = 0.627$] main effects. No significant interaction [$F_{2, 36} = 0.07$, $p = 0.934$] was found. Following left cerebellar stimulation, RTs were significantly slower than those obtained following both right ($p < 0.001$) and sham ($p < 0.001$) cerebellar stimulations, as indicated by post hoc comparisons (Fig. 2a).

Two-way ANOVA on accuracy scores showed a significant task [$F_{1, 36} = 31.63$, $p < 0.001$, $\eta^2_p = 0.468$] main effect, while the effect of stimulation was not significant [$F_{2, 36} = 0.78$, $p = 0.467$]. The interaction was not significant [$F_{2, 36} = 0.73$, $p = 0.488$] (Fig. 2b). These findings indicate the greater difficulty in performing the AMR than EMR task. This difficulty was not affected by both left and right cerebellar stimulations.

Three-way ANOVA on Angular Disparity Index indicated significant stimulation [$F_{2, 18} = 14.94$, $p < 0.001$] and angle [$F_{3, 54} = 27.47$, $p < 0.001$] main effects. View effect and interactions were not significant. Post hoc comparisons on stimulation side factor showed that EMR RTs were significantly slower following left cerebellar stimulation than following right ($p < 0.001$) and sham ($p < 0.001$) cerebellar stimulations. Post hoc comparisons on the angle factor showed that RTs were significantly slower for 180° in comparison to 0° and 90° angles (p always < 0.001) (Fig. 1c).

Discussion

This study measured the performance of adult healthy subjects in two mental rotation tasks, one embodied and one abstract, following inhibitory stimulation of the left or right cerebellar hemisphere. The embodied task required to mentally rotate schematic human body images, while the abstract task required to mentally rotate abstract drawings without affordance properties. Regardless of stimulation conditions, slower RTs and lower accuracy values were obtained in AMR task than in EMR task, suggesting an advantage of egocentric on allocentric representations. Indeed, the kind of stimulus to be rotated appears to be a crucial factor in determining the use of specific strategies. While abstract stimuli trigger the allocentric strategy because their rotation by external forces is easier to imagine, body stimuli mainly trigger the use of the egocentric strategy [2]. Accordingly, we obtained the slowest RTs when the body image to be mentally rotated was presented with an orientation (180°) farthest from the prototypical orientation of the human body, suggesting that participants were performing an egocentric perspective transformation to align their point of view with that of the stimulus [20].

In accordance with the present results, faster RTs and lower error rates were described in an embodied mental rotation task (hand stimuli) in comparison to an allocentric mental rotation task (abstract figures) in correlation with the subjective perception of task difficulty [21]. Additionally, in a short-term spatial memory task, better performances were displayed when an egocentric spatial frame of reference enabled to encode and remember the image locations in comparison to when it was possible to rely merely on allocentric information [22]. However, it has to be taken into account not only the mental rotation strategy but also task differences. Although the timing was the same in both tasks, AMR stimuli contained two images while EMR stimuli depicted a single image to be rotated. Interestingly, the performances of AMR and EMR tasks remained different in the presence of left and right cerebellar stimulations, as depicted by the parallel performances in Fig. 2a, b. Moreover, in both tasks, inhibitory stimulation of the left

Table 1 Group composition in experiments 1 and 2

	Groups	Age
Experiment 1, $n = 21$ [males = 9], education > 13 years	Right cTBS group ($n = 7$)	Range = 22 to 32; mean = 27.43 ± 3.95
	Left cTBS group ($n = 7$)	Range = 24 to 30; mean = 25.86 ± 3.76
	Sham ($n = 7$)	Range = 20 to 35; mean = 26.71 ± 5.09
Experiment 2, $n = 21$ [males = 9], education > 13 years	Right cTBS group ($n = 7$)	Range = 21 to 32; mean = 25.43 ± 3.60
	Left cTBS group ($n = 7$)	Range = 22 to 31; mean = 25.71 ± 3.54
	Sham ($n = 7$)	Range = 24 to 32; mean = 27.43 ± 2.82

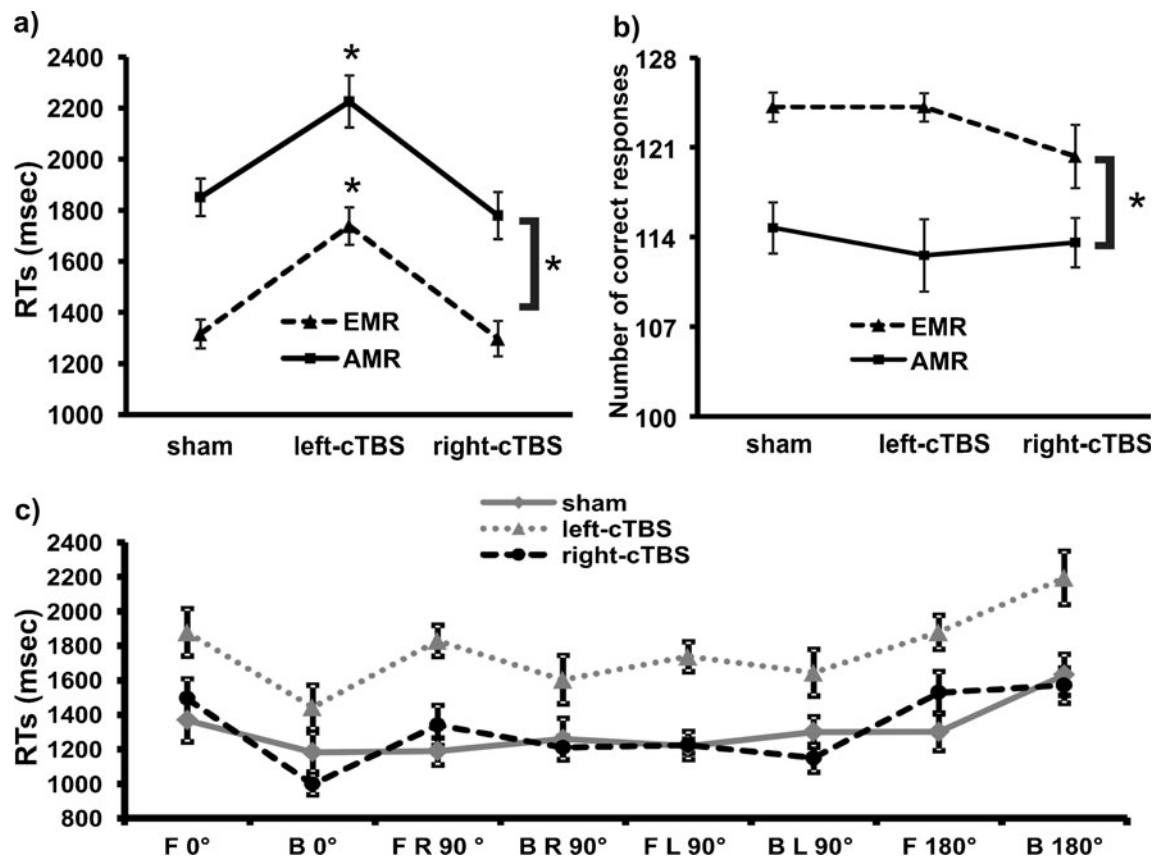


Fig. 2 **a** RTs of the two tasks in milliseconds. In this and in the following figures, bars indicate standard errors. * indicate significance level of $p < 0.001$. Subjects were significantly slower to perform AMR than EMR task. No significant difference was found between right cTBS and sham groups. In left cTBS group, subjects were significantly slower to respond in comparison to the other groups. **b** Accuracy

scores of the two tasks (number of correct responses). Subjects were significantly less accurate to perform the AMR than the EMR task. * indicate significance level of $p < 0.001$. **c** Angular disparity of EMR task. RTs in the three experimental groups according to angles [0°, 90° to the right (R), 90° to the left (L), 180°] and views [frontal (F), back (B)] of the stimulus

cerebellar hemisphere resulted in increased RTs in comparison to right cerebellar hemisphere stimulation. Noteworthy, downregulation of right cerebellar hemisphere excitability did not affect at all performances in both AMR and EMR tasks that appeared identical to those following sham stimulation. These findings demonstrate that left cerebellar hemisphere plays an essential role in mental rotations, regardless of stimuli presented and strategies used, whereas right cerebellar hemisphere seems not to be involved in both mental rotation types. Notably, eventual spreading effects of cerebellar cTBS towards contiguous visual areas may be likely excluded. In fact, if so, a modulatory effect would have been present following both left and right cerebellar stimulations, but this effect did not occur. Furthermore, the cerebellar cTBS could have elicited a vestibular modulation, although no participants reported any vestibular symptomatology. However, if cerebellar cTBS did interact with vestibular system, different modulations of the two MR tasks embodied would have been present. In fact, a recent study reports a

selective influence of vestibular stimulation on the rotation of whole-body reference frames and an interaction with the angle of rotation and vestibular stimulation, demonstrating an increase in facilitation during mental body rotations in a direction congruent with rightward vestibular afferents [23]. Conversely, we did not find RTs and accuracy differences in EMR and AMR tasks following cerebellar cTBS. In spite of it, the eventual interaction of cerebellar cTBS with vestibular system deserves further aimed investigations. The present results fully fit with neuroimaging evidence demonstrating a functional topography organization within the cerebellum, showing the involvement of the left hemisphere in spatial processing and of the right hemisphere in language function [24–26]. Furthermore, lesion studies showed that left cerebellar damage may result in deficits of spatial domain [27, 28]. The left cerebellar lateralization of spatial function reflects the wide bidirectional crossed cerebello-cortical connections with the right parietal regions, known to be involved in mental rotation [29].

In conclusion, cTBS appears a suitable technique to elicit virtual lesions with very short stimulation times and very long after effects. It may provide causative information on cerebellar functional topography to complement neuropsychological and neuroimaging findings [30].

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Conflict of Interest None of the authors has a conflict of interest with respect to the purposes of the present study.

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