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# THE MIRROR NEURON SYSTEM AND MOTOR DEXTERITY: WHAT HAPPENS?

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**Abstract—The mirror neuron system (MNS) is currently one of the most prominent areas of research in neuroscience. Some of the work has focused on the identification of factors that modulate its activity, but until now, no one has tried to identify the effect of motor ability on the MNS regions. The aim of the present work is to study a possible modulation of hand dexterity on the MNS activity.**

**A blocked fMRI experiment has been designed, consisting of an execution condition, where participants must repeatedly perform a precision grasping pantomime, and an observation condition, where the same motor action is passively observed. A conjunction analysis was performed in order to confirm the existence of mirror activity. Moreover, participants were classified depending on their hand dexterity (measured with the Purdue Pegboard Test) as ''High dexterity'' or ''Low dexterity'' and a regression analysis was performed to investigate a possible linear relationship between the degree of dexterity and brain activity in the MNS.**

**The conjunction analysis revealed, as expected, activity in the inferior parietal lobule, a region that constitutes one of the nuclei of the putative MNS and which is consistently activated by intransitive actions. The degree of dexterity only seems to modulate MNS regions during action execution. However, under the observation condition, no linear relationship of hand dexterity in MNS regions was registered in either the comparison between groups, or in the regression analysis.**

**Therefore, the MNS network does not seem to be linearly modulated by the degree of motor dexterity, as occurs with other action-related factors like familiarity.**

**Key words: mirror neurons, motor dexterity, action observation, precision grasping.**

## INTRODUCTION

Mirror neurons are currently one the most prominent research topics. Since their discovery in macaques (di Pellegrino et al., 1992; Gallese et al., 1996), a large number of publications have elucidated many aspects about their features in non-human primates, as well as their presence and organization in humans. Although the presence of single mirror neurons has already been demonstrated in humans (Mukamel et al., 2010), it is more appropriate to talk about the fronto-parietal mirror neuron system (MNS), which is considered as being an action recognition network and, as occurs with mirror neurons, it is activated when an action is executed or observed (Cattaneo and Rizzolatti, 2009; Rizzolatti and Sinigaglia, 2010).

The human MNS presents activity during the observation or execution of transitive and intransitive actions (Iacoboni et al., 1999, 2001; Koski et al., 2003; Jonas et al., 2007; Lui et al., 2008). Nevertheless, there are differences in terms of MNS activation secondary to the transitivity of an action. Generally speaking, the brain activity on the MNS seems to be lower and more restricted to posterior parietal regions for intransitive actions (Rizzolatti and Craighero, 2004).

Apart from the activation of the MNS with transitive or intransitive actions, it is worth noting that one important factor that modulates brain activity within this network is the degree of motor familiarity with the executed or observed action. In this sense, a higher degree of motor familiarity is related to greater activity in MNS regions, independently of whether the action is transitive (Calvo-Merino et al., 2005, 2006; Cross et al., 2006) or intransitive (Plata Bello et al., 2013).

However, a frequent error is to consider motor familiarity as motor dexterity (which is the same as motor ability), because familiarity in motor actions is determined by how often they are performed or observed (Calvo-Merino et al., 2006) but this does not mean that subjects with the same degree of familiarity with a certain action (e.g. football players of different divisions) have the same degree of motor ability for this action performance (normally higher division means higher ability). Dexterity for a certain action means performing a movement skillfully, with velocity and precision, and achieving an efficient manner to perform that action. This aptitude depends on a continuous bidirectional flow of information from the cerebral cortex to the movement effectors and vice versa, via the spinal cord (Kühn et al., 2012).

To the best of our knowledge, no report has tried to identify a possible relationship between motor dexterity

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*Abbreviations:* FWHM, full width at half maximum; FDR, False Discovery Rate; HD, High dexterity; IPG, inferior frontal gyrus; IPL, inferior parietal lobule; LD, Low dexterity; MNI, Montreal Neurological Institute; MNS, mirror neuron system; SMC, sensorimotor cortex; VOIs, volumes of interest.

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(measured by objective and validated tests) with the activity in MNS regions.

Bearing this in mind, the aim of the present work is to identify a possible modulation of hand dexterity in the MNS during the observation and execution of a simple and intransitive finger to thumb opposition task.

## EXPERIMENTAL PROCEDURES

### Subjects

Thirty-one healthy, right-handed (Edinburgh Handedness Inventory (Oldfield, 1971) < 25) and untrained participants were selected (17 women), with an average age of 26.1 (SD = 4.5). Written informed consent was explained and signed. The study was approved by the University of La Laguna Ethics Committee, according to the Declaration of Helsinki.

All participants performed two tests (the ‘‘Letter Cancelation Task’’ and the ‘‘Digit Cancelation Task’’) (Peña-Casanova et al., 2004) to identify any impairment in their attention capabilities and all of them were appropriate candidates for the study.

### Manual dexterity measure

Participants were asked to perform the Purdue Pegboard Test to assess hand dexterity (Tiffin and Asher, 1948). This test consists of a board with two parallel rows with 25 holes per row into which cylindrical pins are placed by the participant. After explanation as well as demonstration of the task and three practice trials, participants were asked to place as many pins into the holes of the perforated board as possible within 30 s of each trial. Three trials per condition were administered with both, the dominant (right) hand and the non-dominant hand; bimanual performance was not allowed. Ability scores were obtained by averaging the number of pins placed correctly during the trials per condition, one for the right hand and another one for the left hand. These scores were used to identify a relationship between the degree of motor dexterity and brain activity associated with the execution or the observation of a finger–thumb opposition task in a further regression analysis which is explained below.

### Data acquisition and processing

Data for the experiment were collected at the Magnetic Resonance for Biomedical Research Service of the University of La Laguna. Functional images were obtained on a 3-T General Electric (Milwaukee, WI, USA) scanner using an echo-planar imaging gradient-echo sequence and an 8-channel head coil (TR = 3000 ms, TE = 21 ms, flip angle = 90°, matrix size = 64 × 64 pixels, 57 slices/volume, spacing between slices = 1 mm, slice thickness = 3 mm). The slices were aligned to the anterior commissure–posterior commissure line and covered the whole cranium. Functional scanning was preceded by 18 s of dummy scans to ensure tissue steady-state magnetization.

A whole-brain three-dimensional structural image was acquired for anatomical reference. A 3D fast spoiled gradient-recalled pulse sequence was obtained with the following acquisition parameters: TR = 10.4 ms, TE = 4.2 ms, flip angle = 20, matrix size = 512 × 512 pixels, .5 × .5 mm in plane resolution, spacing between slices = 1 mm, slice thickness = 2 mm.

After checking the images for artifacts, data were preprocessed and analyzed using Statistical Parametric Mapping software SPM8 (Wellcome Trust Centre for Neuroimaging; http://www.fil.ion.ucl.ac.uk/spm/) and displayed using xjView 8.1 (http://www.alivelearn.net/xjview8/). The images were spatially realigned, unwarped, and normalized to the Montreal Neurological Institute (MNI) space using standard SPM8 procedures. The normalized images of 2 × 2 × 2 mm were smoothed by a full width at half maximum (FWHM) 8 × 8 × 8 Gaussian kernel.

### Study design

Two fMRI runs were performed, one for each condition (execution or observation). The order of the studies was

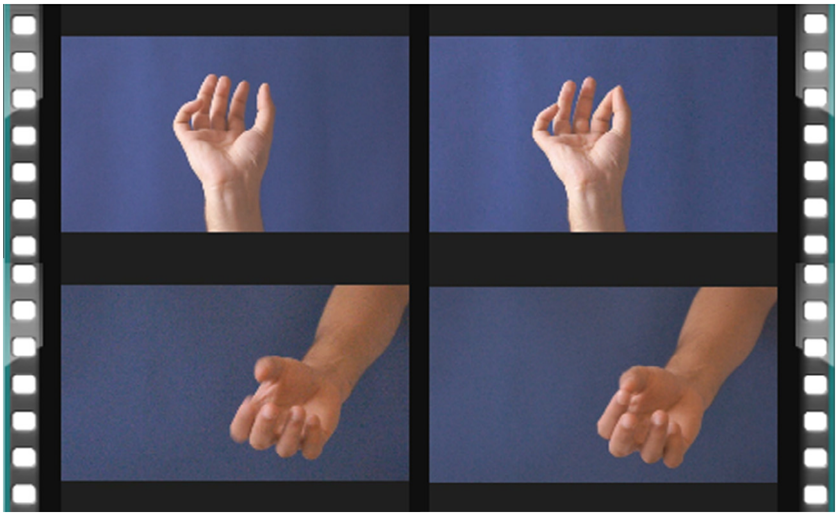

**Fig. 1.** Two frames of the observation condition showing the two visual perspectives: first (up) and third (down) person perspectives.

**Table 1.** Activation peaks with their locations for simple T contrasts and conjunction analysis

| Anatomical region | BA | Peak MNI coordinates | | | *t*-value | *z*-value | Num. voxels |
|---|---|---|---|---|---|---|---|
| | | *x* | *y* | *z* | | | |
| *Execution Index Finger > Control (FDR = 0.05)* | | | | | | | |
| Right Inferior Frontal Gyrus | 40 | 62 | 12 | 14 | 4.09 | 3.61 | 571 |
| Right Precentral Gyrus | 4 | 50 | 4 | 8 | 4.49 | 3.89 | |
| | | 60 | 4 | 34 | 3.47 | 3.15 | |
| Left Precentral Gyrus | | −36 | −22 | 62 | 7.97 | 5.80 | 9970 |
| Left Postcentral Gyrus | 2, 3 | −38 | −30 | 46 | 11.09 | 6.94 | |
| | | −54 | −24 | 52 | 8.84 | 6.16 | |
| Left Inferior Temporal Gyrus | 37 | −48 | −26 | −18 | 4.30 | 3.77 | 43 |
| | | −46 | −64 | −6 | 3.25 | 2.99 | 28 |
| Right Middle Occipital Gyrus | 19 | 50 | −66 | −14 | 4.10 | 3.63 | 161 |
| | | 42 | −76 | −16 | 3.20 | 2.94 | |
| Right Cerebellum | – | 18 | −54 | −32 | 10.50 | 6.75 | 1771 |
| Left Cerebellum | | −4 | −76 | −44 | 3.41 | 3.11 | 45 |
| *Observation Index Finger > Control (FDR = 0.05)* | | | | | | | |
| Right Inferior Temporal Gyrus | 37 | 42 | −62 | −6 | 7.12 | 5.41 | 558 |
| Left Middle Occipital Gyrus | 19 | −46 | −70 | −8 | 6.34 | 5.01 | 213 |
| Left Middle Temporal Gyrus | 37 | −60 | −52 | 4 | 4.26 | 3.74 | |
| | | −56 | −60 | 4 | 4.00 | 3.55 | |
| Left Superior Temporal Gyrus | 39 | −58 | −36 | 10 | 5.18 | 4.34 | 153 |
| | | −62 | −28 | 16 | 4.04 | 3.58 | |
| Right Inferior Occipital Gyrus | 19 | 30 | −86 | −16 | 5.14 | 4.32 | 21 |
| Left Inferior Parietal Lobule | 40 | −34 | −50 | 46 | 4.92 | 4.18 | 111 |
| | | −42 | −34 | 46 | 4.16 | 3.67 | 22 |
| Right Superior Temporal Gyrus | 39 | 52 | −38 | 6 | 4.41 | 3.84 | 65 |
| | | 60 | −34 | 6 | 3.95 | 3.52 | |
| Right Insula | 16 | 56 | −34 | 18 | 4.29 | 3.76 | |
| Right Inferior Parietal Lobule | 40 | 38 | −40 | 38 | 4.14 | 3.65 | 22 |
| | | 34 | −48 | 36 | 3.86 | 3.45 | 19 |
| *Conjunction Execution & Observation Index Finger (FDR = 0.05)* | | | | | | | |
| Left Inferior Parietal Lobule | 40 | −38 | −48 | 46 | 4.84 | 4.43 | |

counterbalanced and both were structured with block designs.

During the execution run, participants were asked to perform the index to thumb opposition task with a frequency determined by a visual cue (a white cross flickering at 1 Hz in the middle of the screen) with the right hand. The subjects' hands were positioned with the palm upwards and the wrist in a neutral position. The left hand was still. The execution blocks lasted 15 s and were repeated 12 times. Instructions to initiate the movement appeared 2 s before the onset of the movement which started when a statement that said "Move index–thumb" disappeared and the above-mentioned white cross started to flicker. The control condition consisted of a static white cross in the middle of the screen. Execution and control conditions were presented in a random order and there was a 3-s fixation (a break with participants watching a black screen) between each condition.

The participants watched videos with the aforementioned movement during the observation run. The videos were projected 12 times for 15 s each. The right-hand finger movements had a frequency of 1 Hz and were randomly presented in a first and a third person perspective (Fig. 1), centered on the screen. The control condition consisted of static photographs of the same hand with the same perspectives. In these photographs the hand was open and with the fingers in a neutral position. Observation and control conditions were presented in a randomized order and there was a 5-s cross fixation (a break with participants watching a black screen with a white cross in the center) between each condition.

## Simple T contrasts

A block design in the context of a general linear model was used, for individual subject analyses (first level), to look for differences in brain activity during the periods of observation and the control condition. The considered contrasts in the analysis were as follows: Index Observation > Control and Index Execution > Control. The first-level contrast images were then used in a random effects group analysis (second level). Group analysis was performed using the random effects approach, using one-sample *t*-test (False Discovery Rate [FDR] = 0.05) with a minimum cluster size of five voxels.

## Conjunction analysis

After the group analysis, a conjunction analysis using the Minimum Statistic compared with the Conjunction Null method (Nichols et al., 2005) was performed to determine voxels activated by observation and execution.

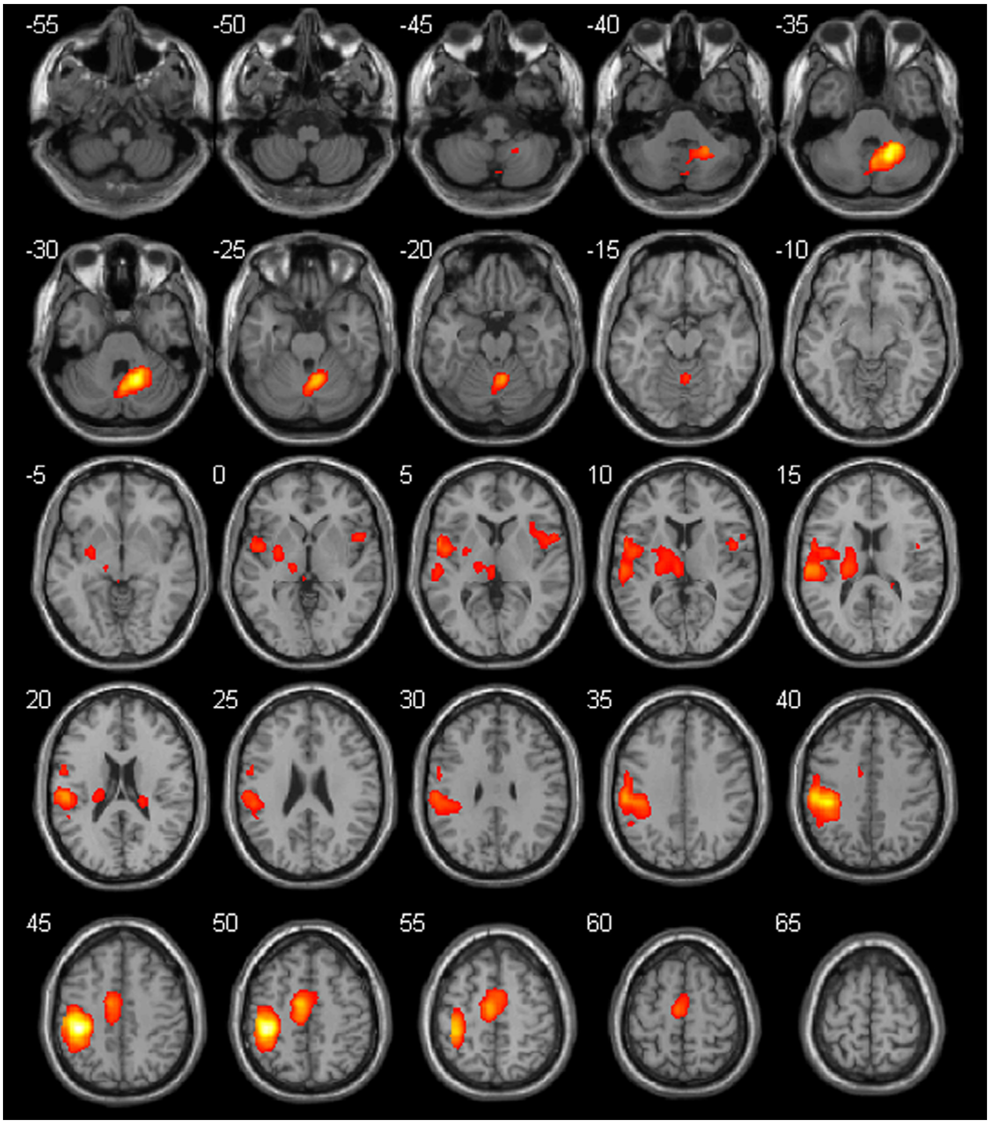

**Fig. 2.** Brain activation pattern during the index–thumb opposition task execution. As expected, motor pathways (including left primary motor area, bilateral premotor area, bilateral basal ganglia and right cerebellum) are where the main activation takes place during the execution of the index–thumb opposition task.

The assumption is that neurons with mirror properties are among those activated during both conditions. Significance was considered with a FDR = 0.05 threshold with a minimum cluster size of five voxels.

## Groups of dexterity

Bearing in mind the results of the Purdue Pegboard Test performed with the right hand, participants were classified into two groups: ‘‘High dexterity’’ (HD) and ‘‘Low dexterity’’ (LD). The median of those results (median = 17.0) was used to make this classification and, therefore, the HD was formed by 13 participants and the LD by 18. Comparisons of the brain activity between dexterity groups in the two conditions of the experiment were performed using a statistical threshold of $p < 0.001$ uncorrected (minimum cluster size of five voxels), due to the absence of significant activity with the corrected threshold. Although using an uncorrected *p*-value is less conservative, it can be considered as an acceptable protection against false positives (Lieberman and Cunningham, 2009).

## Regression analysis

A multiple regression analysis was performed to look for a linear relationship between brain activity during execution or observation of finger–thumb opposition task and the degree of finger dexterity, which was measured with the Purdue Pegboard Test. This regression analysis studied responses across the whole brain at a threshold of $p < 0.001$ uncorrected (corrected threshold did not show significant peaks of activity), with a cluster extent of five voxels. Finally, in order to specifically test the relationship of dexterity with the MNS activity, a regression analysis was also performed for selected volumes of interest (VOIs) located in regions where the

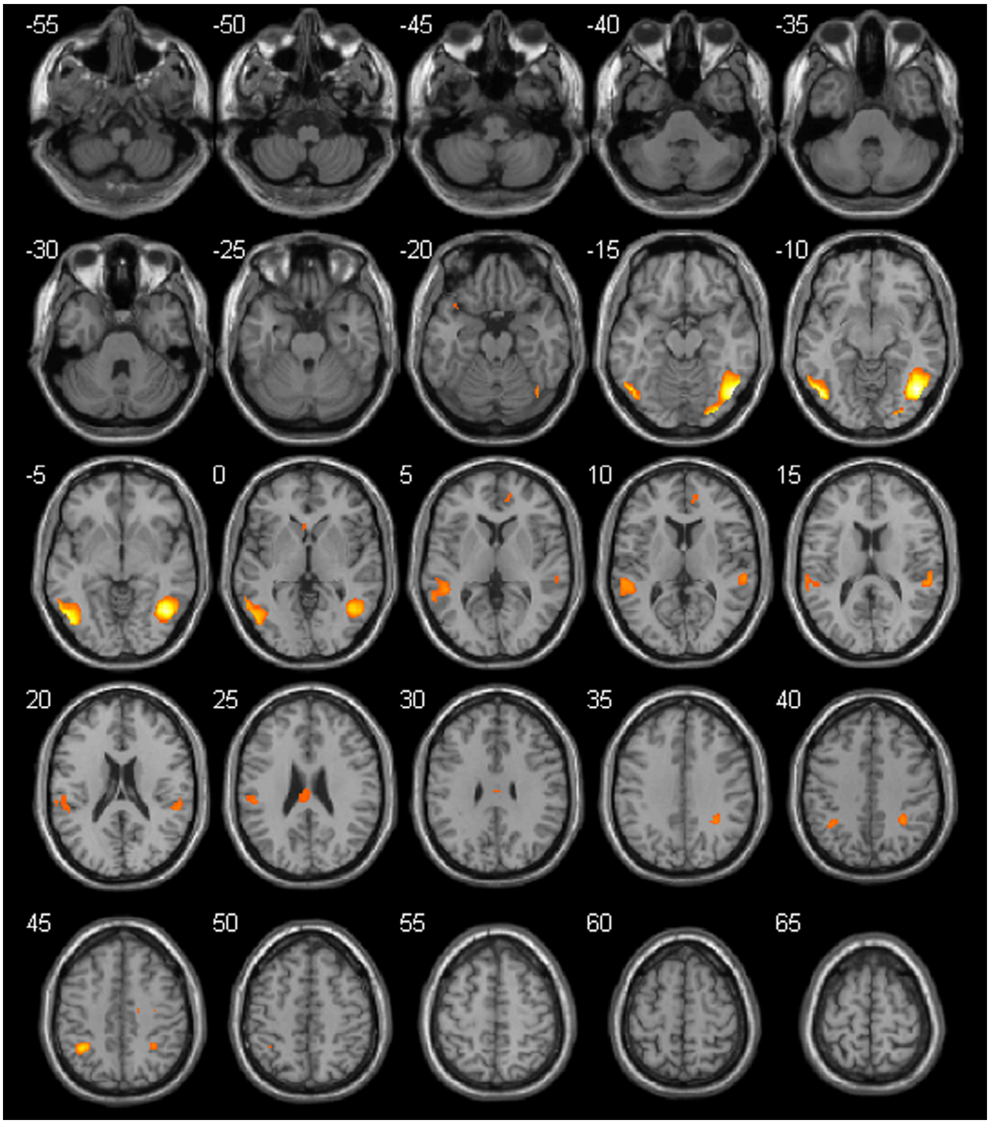

**Fig. 3.** Brain activation pattern during the index–thumb opposition task observation. Bilateral temporal and occipital regions are intensively activated during the opposition task observation. Bilateral posterior parietal activity is also present, corresponding with the inferior parietal lobule.

conjunction analysis revealed activation in both execution and observation conditions, which is considered to be part of the MNS. The VOIs around these coordinates corresponded to 10-mm spheres around the specified peak voxels and the significance within this analysis was FDR = 0.05.

## RESULTS

### Descriptive data on dexterity measurement results

The participants placed on average 16.8 (SD = 2.0) pins with their right hand and 14.5 (SD = 2.0) with their left hand. Differences between right and left hands were expected based on the right handedness of the participants. This difference was statistically significant ($t = 7.295$, $p < 0.001$) and a positive correlation within subjects existed between the two variables (Pearson Correlation = 0.627, $p < 0.001$). Furthermore, there was a statistically significant difference between the means of the Purdue results with the right hand between HD (mean = 18.8; SD 1.0) and LD (mean = 15.4; SD = 1.4) groups ($t = 7.732$, $p < 0.001$).

### Execution and observation simple contrasts

The execution of the index–thumb opposition task preferentially activated motor pathways, with higher BOLD signal in the left sensorimotor cortex (SMC) and right cerebellum (Table 1; Fig. 2). It should be noted that the cluster whose peak of activity was located in the left SMC also extended over the left inferior parietal lobule (IPL) (Fig. 2).

On the other hand, observation of the index–thumb opposition task led to higher BOLD signal in both brain hemispheres in temporal, parietal and occipital regions (Table 1; Fig. 3).

### Conjunction analysis

Only one peak of activity in the left IPL reached significance with corrected $p$-values in the conjunction

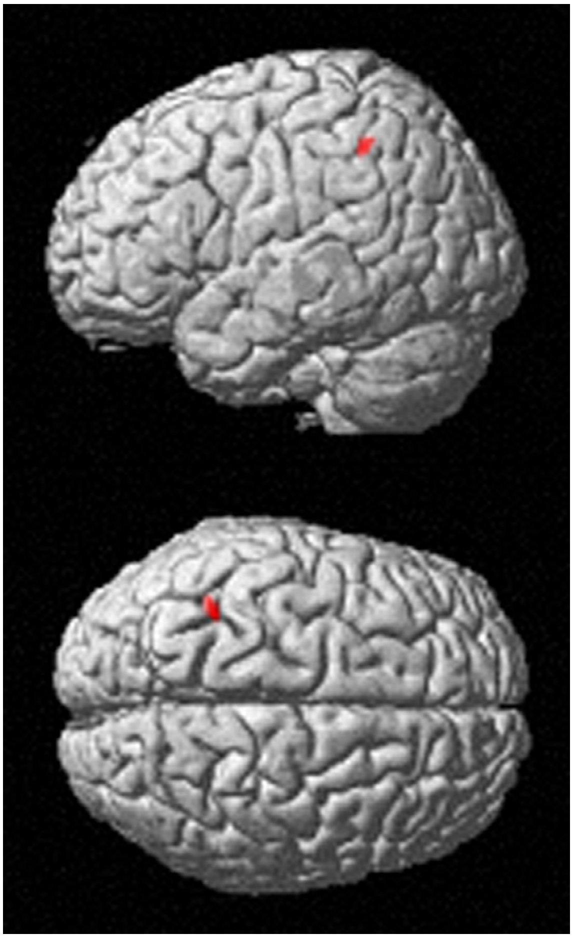

**Fig. 4.** Common activation during execution and observation of the index–thumb opposition task. A unique cluster, located in right IPL, is shown in the conjunction analysis between execution and observation with the selected threshold (FDR > 0.05; $k = 5$).

analysis between execution and observation contrasts of the index–thumb opposition task (Table 1; Fig. 4).

### Dexterity groups and regression analysis

As can be seen in Table 2, during the execution of the finger–thumb opposition task, the HD group showed higher activity than the LD group (High dexterity > Low dexterity) in the bilateral inferior frontal gyrus (IFG), which is located in premotor regions and constitutes a part of the putative MNS (Fig. 5). When the opposite contrast was tested (Low dexterity > High dexterity) no MNS regions showed higher activation for the LD group which only presented higher activity than the HD group in the right insula and the right precuneus. On the other hand, during the observation condition, the HD group showed higher activity in the right temporal lobe than the LD group, whereas the opposite contrast did not show significant peaks of activity with the selected threshold (Table 3).

The regression analysis between brain activity and degree of grasping ability with the right hand (Table 4; Figs. 5 and 6) showed positive relationships with different regions under the execution and the observation conditions. Although frontal areas presented such a relationship in both conditions, in the observation condition they were located in the medial frontal/cingulate gyrus, while in the execution condition they were clearly located in motor areas (primary and premotor areas) ($p$-value < 0.001 uncorrected). Brain activity even showed a positive relationship with right finger dexterity during the execution condition in the right cerebellum. Finally, it is worth mentioning that the strongest positive relationships between the activity in both conditions (execution and observation) and the manual dexterity measure were found in the right hemisphere and both conditions activated the right middle temporal gyrus (MTG).

The VOI analysis in the coordinates of the main peak in the conjunction analysis [−38, −48, 46] did not reveal any significant activity with the selected threshold in the MNS regions. Furthermore, no correlation existed with the Purdue Pegboard Test data from the left hand and brain activity for execution and observation tasks with the selected statistical threshold.

## DISCUSSION

### Activation of the MNS

Most of the neuroimaging studies focusing on the MNS have used paradigms based on the observation of transitive actions, but an activation of the MNS network has also been demonstrated with intransitive actions (Iacoboni et al., 1999, 2001; Buccino et al., 2001; Koski et al., 2003; Jonas et al., 2007; Lui et al., 2008). However, different patterns of brain activity exist between transitive and intransitive actions. While ventral premotor cortex and posterior parietal areas showed higher activity for transitive actions (Buccino et al., 2001; Filimon et al., 2007), the posterior parietal regions are activated more consistently for intransitive actions (Cattaneo and Rizzolatti, 2009).

The results of the present research agree with this previous observation. Although activity in several regions belonging to the MNS showed an increase during both execution and observation conditions (Table 1; Figs. 2 and 3), the conjunction analysis revealed that only the left IPL presented shared voxels of activity for both conditions (Fig. 4). The IPL is an important core region of the MNS (Cattaneo and Rizzolatti, 2009; Gazzola and Keysers, 2009) and it is also implicated in the identification and the monitoring of the kinematics features of an action (Jäncke et al., 2001; Castiello, 2005; Haller et al., 2009), especially for grasping movements (Castiello, 2005).

On the other hand, the premotor regions are also involved in grasping actions and it seems that their activation is related to the possibility of an interaction with an object (e.g. grasping a tea cup) (Jeannerod et al., 1995; Binkofski et al., 1998, 1999; Ehrsson et al., 2000; Kuhtz-Buschbeck et al., 2001; Astafiev et al., 2003; Theorin and Johansson, 2007) as well as the prediction of other associated actions (e.g. drinking or tidying) (Ramnani and Miall, 2004; Iacoboni et al., 2005). In this sense, special consideration has been made for the

**Table 2.** Activation peaks with their locations for simple T contrasts for Execution condition in different groups of dexterity

| Anatomical region | BA | Peak MNI coordinates | | | *t*-value | *z*-value | Num. voxels |
|---|---|---|---|---|---|---|---|
| | | *x* | *y* | *z* | | | |
| *Execution Index Finger > Control (Higher dexterity group) (FDR = 0.05)* | | | | | | | |
| Right Cerebellum | – | 18 | −56 | −32 | 9.30 | 6.28 | 1226 |
| Left Postcentral Gyrus | 2, 3 | −38 | −34 | 60 | 6.62 | 5.13 | 2141 |
| | | −38 | −28 | 46 | 6.58 | 5.10 | |
| | | −56 | −28 | 50 | 5.18 | 4.33 | |
| Left Inferior Temporal Gyrus | 37 | −52 | −28 | −20 | 5.51 | 4.52 | 81 |
| Left Postcentral Gyrus | 2, 3 | −56 | −22 | 18 | 5.49 | 4.51 | 405 |
| Left Superior Temporal Gyrus | 39 | −50 | −36 | 14 | 4.16 | 3.65 | |
| Right Inferior Frontal Gyrus | 44 | 62 | 14 | 14 | 4.32 | 3.77 | 121 |
| | | 52 | 8 | 6 | 3.76 | 3.37 | |
| Left Medial Frontal Gyrus | 37 | −4 | −10 | 56 | 4.16 | 3.65 | 278 |
| Right Superior Frontal Gyrus | 6 | 2 | 2 | 68 | 4.06 | 3.58 | |
| | | 2 | 10 | 62 | 3.80 | 3.39 | |
| *Execution Index Finger > Control (Lower dexterity group) (FDR = 0.05)* | | | | | | | |
| Left Postcentral Gyrus | 2, 3 | −50 | −26 | 54 | 8.77 | 6.08 | 5361 |
| | | −38 | −30 | 48 | 8.55 | 6.00 | |
| | | −40 | −34 | 58 | 8.20 | 5.85 | |
| Right Cerebellum | – | 18 | −54 | −32 | 7.34 | 5.47 | 790 |
| Right Insula | 16 | 42 | −2 | 14 | 5.19 | 4.33 | 122 |
| Left Insula | | −42 | −6 | 12 | 5.08 | 4.26 | 837 |
| Left Precentral Gyrus | 4 | −52 | 4 | 8 | 4.27 | 3.73 | |
| *Execution Index Finger (Higher dexterity vs. Lower dexterity) (p-value uncorrected = 0.001)* | | | | | | | |
| Higher dexterity > Lower dexterity | | | | | | | |
| Left Inferior Frontal Gyrus | 44 | −42 | 4 | 30 | 4.37 | 3.80 | 63 |
| Right Inferior Frontal Gyrus | | 56 | 28 | 20 | 3.92 | 3.49 | 11 |
| Left Middle Frontal Gyrus | 6 | −38 | 0 | 58 | 3.55 | 3.21 | 6 |
| Right Inferior Temporal Gyrus | 37 | 64 | −56 | −14 | 3.54 | 3.20 | 7 |
| Higher dexterity < Lower dexterity | | | | | | | |
| Right Insula | 16 | 40 | −4 | 14 | 4.32 | 3.76 | 43 |
| Right Precuneus | 7 | 22 | −46 | 34 | 3.98 | 3.53 | 15 |

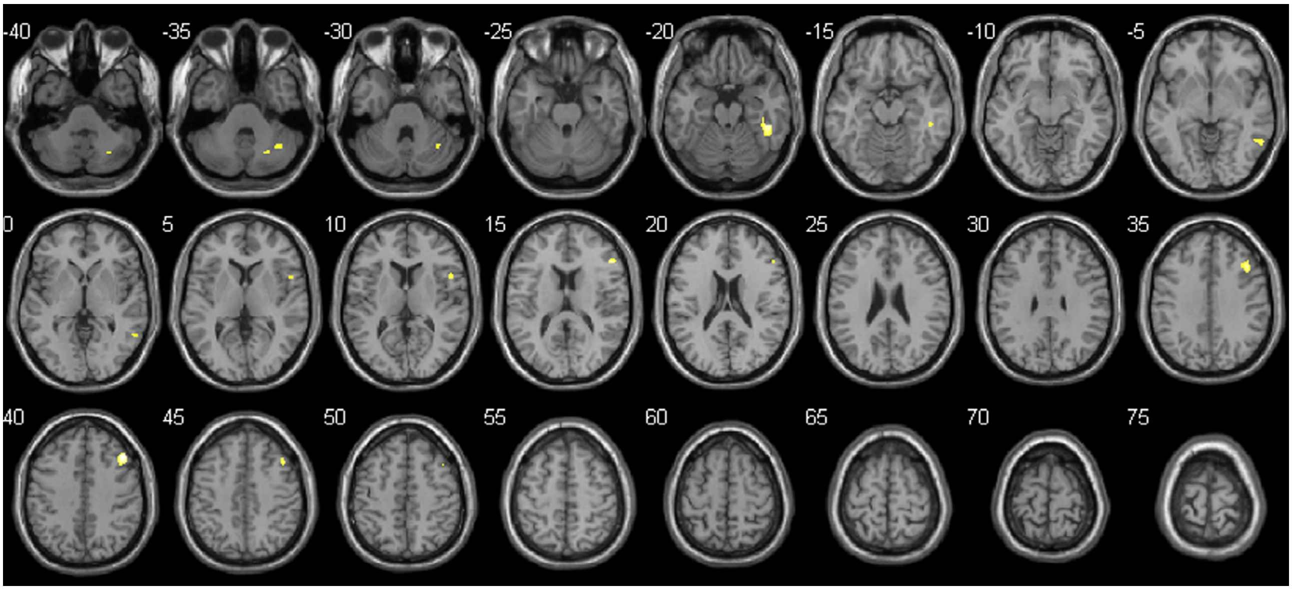

**Fig. 5.** Regression analysis between dexterity scores and BOLD signal during finger–thumb execution. A relationship between a higher degree of dexterity, determined by the Purdue Pegboard Test, and BOLD signal during intransitive grasping execution is presented in the right premotor regions and in the ipsilateral cerebellum.

**Table 3.** Activation peaks with their locations for simple T contrasts for observation condition in different groups of dexterity

| Anatomical region | BA | Peak MNI coordinates | | | *t*-value | *z*-value | Num. voxels |
|---|---|---|---|---|---|---|---|
| | | *x* | *y* | *z* | | | |
| *Observation Index Finger > Control (Higher dexterity group) (FDR = 0.05)* | | | | | | | |
| Left Middle Occipital Gyrus | 37 | −54 | −64 | −10 | 6.00 | 4.80 | 1262 |
| Left Superior Temporal Gyrus | 39 | −50 | −40 | 10 | 5.87 | 4.73 | |
| Left Middle Temporal Gyrus | 37 | −62 | −48 | 4 | 3.70 | 3.32 | |
| Right Middle Temporal Gyrus | | 52 | −50 | −12 | 5.78 | 4.68 | 1099 |
| Right Inferior Temporal Gyrus | | 58 | −60 | −16 | 5.69 | 4.62 | |
| Right Inferior Parietal Lobule | 40 | 34 | −40 | 38 | 4.39 | 3.81 | 141 |
| | | 40 | −52 | 50 | 3.97 | 3.52 | |
| Right Postcentral Gyrus | 2, 3 | 58 | −22 | 16 | 4.25 | 3.72 | 102 |
| *Observation Index Finger > Control (Lower dexterity group) (FDR = 0.05)* | | | | | | | |
| Right Middle Occipital Gyrus | 37 | 46 | −68 | −12 | 5.56 | 4.55 | 444 |
| Right Inferior Occipital Gyrus | 19 | 32 | −86 | −14 | 3.79 | 3.39 | |
| Right Middle Occipital Gyrus | 37 | 40 | −82 | −16 | 3.46 | 3.14 | |
| Left Inferior Temporal Gyrus | | −48 | −72 | −2 | 4.88 | 4.14 | 311 |
| Left Middle Occipital Gyrus | | −44 | −70 | −10 | 4.61 | 3.96 | |
| | | −50 | −76 | −10 | 4.38 | 3.81 | |
| Left Superior Temporal Gyrus | 39 | −54 | −38 | 10 | 4.35 | 3.78 | 195 |
| Left Insula | 16 | −46 | −36 | 18 | 3.98 | 3.53 | |
| *Observation Index Finger (Higher dexterity vs. Lower dexterity) (p-value uncorrected = 0.001)* | | | | | | | |
| Higher dexterity > Lower dexterity | | | | | | | |
| Right Superior Temporal Gyrus | 39 | 56 | 10 | −16 | 4.10 | 3.61 | 17 |
| Right Middle Temporal Gyrus | 37 | 56 | −50 | −14 | 4.07 | 3.59 | 36 |
| Right Inferior Temporal Gyrus | | 58 | −60 | −16 | 4.07 | 3.59 | 6 |
| Left Cerebellum | – | −20 | −48 | −32 | 3.80 | 3.39 | 13 |
| Right Precentral Gyrus | 4 | 46 | −14 | 58 | 3.74 | 3.35 | 7 |
| Right Middle Temporal Gyrus | | 56 | 2 | −34 | 3.70 | 3.32 | 6 |
| Higher dexterity < Lower dexterity | | | | | | | |
| – | – | – | – | – | – | – | – |

**Table 4.** Regression analysis between BOLD signal in each experimental condition and the score in the Purdue Pegboard Test

| Anatomical region | BA | Peak MNI coordinates | | | *t*-value | *z*-value | Num. voxels |
|---|---|---|---|---|---|---|---|
| | | *x* | *y* | *z* | | | |
| *Linear regression between Execution and Purdue Pegboard Test scores (p-value uncorrected < 0.001)* | | | | | | | |
| Right Middle Frontal Gyrus | 9 | 46 | 26 | 40 | 4.73 | 4.02 | 149 |
| | | 36 | 50 | 14 | 3.58 | 3.22 | 7 |
| Right Inferior Frontal Gyrus | 44 | 52 | 30 | 16 | 4.28 | 3.72 | 24 |
| Right Precentral Gyrus | 4 | 52 | 12 | 8 | 3.89 | 3.45 | 29 |
| Right Middle Temporal Gyrus | 37 | 60 | −56 | −4 | 3.83 | 3.40 | 68 |
| Right Cerebellum | – | 38 | −58 | −30 | 3.67 | 3.29 | 27 |
| | | 26 | −66 | −34 | 3.63 | 3.26 | 25 |
| | | 32 | −64 | −44 | 3.54 | 3.19 | |
| *Linear regression between Observation and Purdue Pegboard Test scores (p-value uncorrected < 0.001)* | | | | | | | |
| Right Anterior Cingulate Gyrus | 24 | 10 | 36 | 30 | 4.44 | 3.83 | 24 |
| Right Middle Temporal Gyrus | 37 | 58 | −52 | −4 | 3.77 | 3.36 | 10 |
| Left Anterior Cingulate Gyrus | 24 | −6 | 46 | 26 | 3.60 | 3.23 | 11 |
| Right Anterior Cingulate Gyrus | | 2 | 46 | 24 | 3.49 | 3.15 | |

right IFG as a mirror region involved in subsequent actions prediction (Iacoboni et al., 2005). The paradigm of the present work consisted of an intransitive action and there was not any subsequent action to predict, thus the absence of activity in premotor regions is coherent with the finding of Iacoboni et al. (2005).

Therefore, the main activity of the MNS during the execution and the observation of a precision grasping pantomime seem to be located in the IPL and not in premotor areas.

## Familiarity does not mean dexterity

Previous research has focused on the factors modulating the activity in the MNS, but no one has elucidated the effect of dexterity in these regions. There is probably

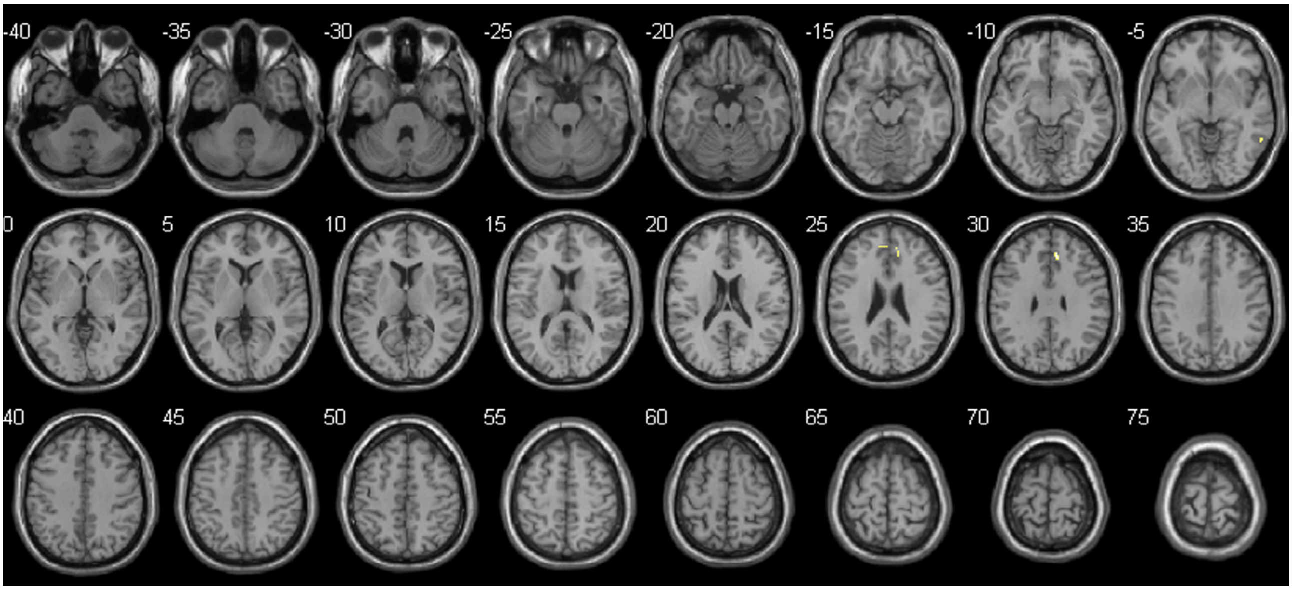

**Fig. 6.** Regression analysis between dexterity scores and BOLD signal during finger–thumb observation. The BOLD signal in the medial frontal cortex and the right MTG show the relationship with the score in the Purdue Pegboard Test. None of these regions has been considered as the core of the MNS.

some confusion between the terms ''familiarity'' and ''dexterity'', but they should not be considered as the same concepts. As regards familiarity, Calvo-Merino et al. (2005) made a differentiation between visual and motor familiarity, considering that a group of ballet dancers has the same degree of visual familiarity with all ballet-specific movements, but a different degree of motor familiarity when specific gender actions were considered (Calvo-Merino et al., 2005). This means that visual familiarity comes from repeatedly observing a certain action, whereas motor familiarity needs practice. However, if subjects with the same motor familiarity (e.g. football players) are considered, differences should exist between those players who present higher dexterity and those who have lower dexterity.

Some studies have tried to identify differences in brain activation produced by the degree of dexterity (Hund-Georgiadis and von Cramon, 1999; Jäncke et al., 2000). However, these studies used two different dexterity groups (experts in something and novices) that may not be suitable because of the different degree of motor familiarity between groups. In this sense, one cannot be sure whether the results they obtained were more related to the different motor familiarity than to the real effect of dexterity in brain activation.

In any case, it can be argued that a higher degree of familiarity could be associated with a higher degree of dexterity, but the present study has tried to avoid this confusion factor. In other words, the index–thumb opposition task, which is the pantomime of a precision grasping finger action, may be considered as a familiar action for all healthy subjects, because the use of other fingers for this specific action is uncommon (Napier, 1956) and everybody may be assumed to present the same visual or motor familiarity with this fundamental movement for humans (Napier, 1956; Castiello, 2005).

Consequently, taking these aspects into account, the paradigm selected here allows the objective classification of the participants into two motor dexterity groups, and thus this approach would seem to be appropriate to meet the aim of the present work.

## No effect of dexterity in the MNS

As described in the results section, only during the execution condition, the degree of dexterity presented modulation of regions belonging to the MNS areas (Tables 2–4; Figs. 4 and 5).

The implication of the premotor and posterior parietal regions (nonprimary frontoparietal network) during the execution of precision grasping actions has been previously defined (Kuhtz-Buschbeck et al., 2001). Moreover, Galléa et al. (2005) found that, during a dexterity task with precision variation of force control, a relationship exists between sensory processing and action monitoring (Galléa et al., 2005). In addition, fine manipulation of objects, an action requiring certain hand and finger dexterity, also leads to an activation of the nonprimary frontoparietal network (Jäncke et al., 2001; Stoeckel et al., 2003). All of these authors agree that premotor areas are clearly involved in fine control of dexterity tasks. In the same way, the present research shows that the HD group presented larger clusters of activation in premotor regions and there was a positive correlation in the regression analysis between BOLD activity and the Purdue Pegboard Test score in the right IFG. Taken together, the results of the present work agree with the previous research (Galléa et al., 2005): higher premotor activity is shown when the actor presents higher dexterity during action execution.

On the other hand, during the action observation condition, no region belonging to the MNS presented any modulation produced by the degree of dexterity. Moreover, neither the right nor the left IPL (one of the main regions of the MNS) presented significant differences of activation between HD and LD groups in both conditions (observation and execution). Furthermore, no correlation with dexterity was found for this area, even in the VOI analysis.

Therefore, unlike familiarity, the degree of motor dexterity only seems to modulate brain activation in the MNS during action execution and not during action observation, so motor dexterity may not be a modulator of the MNS.

## CONCLUSION

The MNS presents activity during the execution and the observation of intransitive actions. This activity is mainly located in the posterior parietal regions.

Moreover, different brain activity patterns related to the degree of finger dexterity have been described during the execution and the observation of motor actions. The modulation of MNS regions by motor dexterity seem to be present only during action execution, but not during action observation. Consequently, motor dexterity may not be considered as a modulator of the MNS activity.

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