Lateralized activation of the motor system to the observation of left and right hand actions[1]

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A primary feature of the human motor system is its crossed organization (e.g. left motor cortex controls right hand). In the present study MEG recordings were used to investigate whether observation of left and right hand finger movement results in lateralized activation of the motor cortex. Lateralized activation in the form of a lateralized readiness field was found over the motor cortex for both executed and observed finger movements. These results suggest that the basic neural organization that controls left and right limb movements during execution may be used to effectively differentiate between left and right movements of others in action observation.

Keywords: mirror neurons, action observation, cross organization, primary motor cortex, magnetoencephalography, lateralized readiness field.

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Introduction

To understand other people's behavior we have to know what their intentions are, their emotional state of mind, and their goals. For this we have to be able to read and interpret their movements, gestures, and facial expressions. Area F5 of the monkey brain contains neurons, called mirror neurons that are active during both goal directed execution and observation of actions (Rizzolatti et al., 1996). Comparable effects have been reported in different parts of the human motor system, i.e. the inferior frontal gyrus, primary motor cortex, and the inferior parietal lobule (Fadiga et al., 1995; Buccino et al., 2004). It is suggested that the mirror neuron system in humans could play a major role not only in our understanding of other people's behavior but also in imitation, learning of motor skills (Jeannerod, 2001), and even language (Rizzolatti and Arbib, 1998).

With respect to action observation neuroimaging results consistently find that motor activation during action observation mirrors the activation that is typically found during action execution. Interestingly, it is not known whether left and right limb movements are represented separately in action observation. That is, it is not known whether the crossed organization of the motor system (Cheyne et al., 1994) that is evident in motor performance (e.g. left motor cortex controls right hand) is also used for the observation of other people's motor actions. Previous studies using transcranial magnetic stimulation (TMS) of the primary motor cortex or EEG recordings over the left and right lateralized motor areas, suggest that there might be lateralized activation of the motor cortex during action observation (Aziz-Zadeh et al., 2002, van Schie et al., 2004).

In this study we would like to focus on this aspect of action observation by answering the following question. Is our motor system sensitive for the laterality of movements during action observation? To study this phenomenon we let our subjects execute and observe left and right hand finger movements. For the observation task pictures were presented of hands performing the same actions that subjects performed in the execution condition. Images of recorded movement are known to have a comparable effect to observation of a live actor (Järveläinen et al., 2001). Brain activity during execution and observation conditions was recorded with 151 MEG channels, and laterality of motor activity in conjunction with left and right hand movement was determent by calculating the magnetic equivalent of the lateralized readiness potential (LRP) (Praamstra et al., 1999). It is hypothesized that activation over the left and right motor cortices will lateralize, as a function of the laterality of the observed hand movements.

Materials and Methods

Subjects

12 healthy subjects (3 female and 9 male, ages between 22 and 33), of which 6 left-handed and 6 right-handed took part in the experiment. All had normal or corrected-to-normal vision. Most subjects were selected from the people working at the F.C. Donders centre, and most of them had prior experience with MEG or other type of neuroimaging experiments. Subjects were informed beforehand about the experimental procedure, and were paid 6 euros per hour. Subjects gave their informed consent, and procedures were approved by the F.C. Donders centre.

Apparatus and stimuli

During the experiment the subjects were seated in a 151-channel axial-gradiometer whole-head MEG system (CTF Systems Inc., Vancouver, Canada) in a magnetically shielded room. In parallel with MEG, EEG was recorded (28-channel, CTF Systems Inc.). Measurements from the locations C3 and C4 were recorded by electrodes located over the left and right motor cortices respectively, and FCz over medial frontal cortex, referenced to both mastoids. To keep track of finger movements during the experiment EMG was recorded bipolarly. For the EMG, electrodes were placed on both arms over the extensor of the index finger halfway on the upper side of the lower arms. Horizontal and vertical eye signals were recorded bipolarly, and trials with eye movements and blinks were rejected from the analyses. All channels were recorded with acquisition software on a Linux computer at a sampling rate of 600 samples per second.

Two LUMITouch (Photon Control Inc. Baxter, Canada) optical button boxes (one for each hand) were used for recording and monitoring subjects' responses, and for triggering the stimulus presentation computer. The two button boxes were placed next to each other in front of the subject. The position of the boxes was adjusted so that the subjects had their arms in a comfortable position. The subject's elbows were supported by cushions to minimize movement of the upper arm to prevent movement artifacts. The index fingers of the subject's left and right hand were placed in a bend posture in front of the buttons to minimize hand movements, and to make sure that contralateral movements were not obstructed by the presence of the other hand.

Stimuli were projected onto a semi-transparent screen with a size of 42x32 cm placed at a distance of 70 cm in front of the subject. Two types of stimuli were shown, cue stimuli indicating how to respond, and response stimuli showing the actual response. The response stimuli show the same button boxes used during the execution task together with two hands shown from a first person perspective. The cue stimuli and response stimuli respectively had a size of 112x112 and 300x174 pixels, a spatial resolution of 72 dpi, and a 24 bit color depth.

Procedure

The experiment existed of 11 execution and 11 observation blocks containing 80 trials each. The blocks were presented in an alternating fashion, and the starting order was counterbalanced over the subjects. The first two blocks were used for practice and were not recorded. The duration of the experiment was approximately 75 minutes.

During the execution task the participants were asked to respond both fast and accurately to the cue stimuli and to try to avoid correcting initial errors. During this task as shown in Figure 1, the cue stimulus was shown for 200ms, and after the response offset recorded by a button press there was a 2000ms interval before the next cue stimulus came on. During all blocks a fixation cross was continuously aligned to the centre of the cue stimulus. The cue stimulus consisted of a square in which four dots were placed. The two dots in the bottom half of the square indicated the starting positions of the two index fingers, and the two dots in the top half of the square indicated the two target positions. The colors of the square and dots could either be red or green. The dot in the bottom half with the same color as the square indicates the index finger that should move, and the dot in the top half with the same color as the square indicates the target that the finger should go to. In case of the cue shown in Figure 1 the right index finger should move to the right target. Eight different cue stimuli could be presented, depending on the response hand (50% left finger movements and 50% right finger movements), movement direction (50% ipsilateral and 50% contralateral finger movements), and color (50% red and 50% green).

The order of events in the observation task was chosen to be similar to the execution condition. Subjects were first presented with a 200ms cue stimulus showing the same four colored dots presented in a colored frame (see Figure 1). In the lower part of the screen, hands were shown continuously in a starting posture. 400ms after the onset of the cue stimulus, the starting posture of the hands was replaced by a different photo showing a response of the left or right hand (ipsi- or contralateral movement). The response stimulus stayed on for 300 ms after which the hands returned to their starting position. After the response there was a 2000 ms interval before the next trial was presented. To make sure that subjects kept their attention on the screen, and observed responses of the virtual actor, the subject's task was to detect and count occasional errors (e.g. wrong hand moved, or hand moved to the wrong target, or both). To make the task of the observer as unambiguous as possible the square of the cue stimulus was always yellow. Four types of responses were shown: in 70% of the trials a 'correct response' was shown in which the correct index finger went to the correct target, in 10% of the trials a 'hand error' was shown in which the index finger of the wrong hand went to the correct target, in 10% of the trials a 'target error' was shown in which the index finger of the correct hand went to the wrong target, and in 10

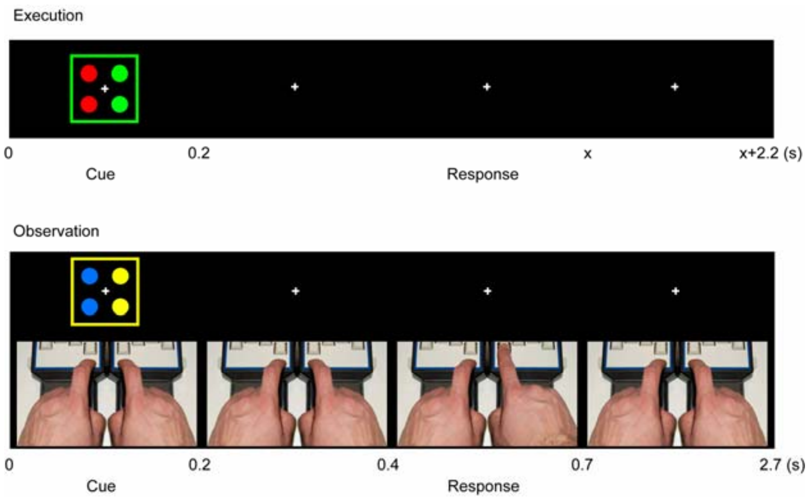

Figure 1. Top, execution task. The cue stimulus is on for 200ms followed by a response. After the response offset (x) there is a 2 sec. interval. Bottom, observation task. The cue is presented for 200ms followed by an interval of 200ms, after which the response stimulus is shown for 300 ms, followed by an interval of 2 sec.

% of the trials a 'hand&target error' was shown in which the index finger of the wrong hand went to the wrong target.

Each block started with 8 correct trials, after which the remaining 72 trials were presented in a random order. Subjects were asked to count and report the number of observed errors at the end of each block. The number of errors was the same for each block. The reports show small deviations in counted errors for each block, which suggests that the subjects were not aware that the number of errors was fixed.

During both tasks subjects were asked to keep their eyes on the fixation cross and to minimize blinking. After each block subjects received feedback about their blinking behavior if necessary. There were pauses between the blocks in which subjects were allowed to rest. During both tasks and during pauses subjects were asked to keep their head movements to a minimum.

Data analysis

Behavioral data was analyzed for reaction times, and response types. Reaction times reflect the time between the onset of the cue stimulus and the subsequent button press. Analysis of the EMG data was used to determine which hand was moved for each trial. This was done by calculating the average absolute power for each EMG signal in a time window of 500 ms prior to the button press. The strongest signal corresponded to the responding hand. The signal of the moving hand had to be at least twice the power of the stationary hand, otherwise the trial was marked as ambiguous and discarded during preprocessing. The target of the finger movement was determined by which button was pressed. Four types of responses were classified: (i) a 'correct response' in which the correct index finger went to the correct target, (ii) a 'hand error' in which the index finger of the wrong hand went to the correct target, (iii) a 'target error' in which the index finger of the correct hand went to the wrong target, and (iv) a 'hand&target error' in which the index finger of the wrong hand went to the wrong target.

Analysis of EEG data was done for 7 subjects. Due to excessive noise the EEG signals of 5 subjects had to be discarded from the analysis. Preprocessing involved rejection of trials containing eye artifacts, rejection of trials containing ambiguous responses, and baseline correction over a period of 500 to 400 ms prior to the response offset. After preprocessing the trials were averaged per condition, channel, and separate for left and right hand movements. Averages were used for calculating the LRP according to the subtraction averaging method: LRP = [left hand(erpC4 - erpC3) + right hand(erpC3 - erpC4)]/2. Negative values of the LRP indicate relative activation of the hemisphere contralateral to the correct response hand, and positive values indicate relative activation of the opposite hemisphere associated with the incorrect response hand (Coles, 1989).

The same preprocessing, averaging, and subtraction averaging method that were done for the EEG recordings were also used for the analysis of MEG data. For the MEG data we will refer to lateralized readiness field (LRF) instead LRP because this signal reflects magnetic fields instead of electrical potentials. Before applying the subtraction averaging method, MEG data was converted to planar gradient (Bastiaansen and Knösche, 2000). Instead of C3 and C4 the LRF was calculated for all possible left and right mirror symmetrical channel combinations. In this way a complete topographical plot of the lateralized activation is derived with the left and right sides of the plot showing activation in opposite polarity, but with a symmetrical distribution. In order to allow a direct comparison with LRP effects the results and discussion will focus on effects over the right side of the topographical plots in which relative activation over the hemisphere contralateral to the response hand is indicated as a negative value. Positive values shown in red however indicate relative activation over the other hemisphere in association with the incorrect response hand.

Statistics

Statistics performed on the EEG data was done with a paired-samples t-test using SPSS statistical software. Statistics performed on the MEG data was done by means of randomization test statistics (Maris, 2004), to handle the multiple comparisons problem that arises when performing statistics on a high dimensional dataset (151 channels; 600 Hz sampling). All preprocessing for EEG and MEG data and statistical tests on MEG data were done using Fieldtrip (a biological data analysis software package running in Matlab; www.ru.nl/fcdonders/fieldtrip).

Results

Execution condition

The analysis of behavioral data showed that subjects' reaction times for correct (93.75%, 757 ms) and incorrect (6.25%, 833 ms) responses were not significantly different ($t11 = -1.807$, $P = .098$). Incorrect responses were found in the form of hand errors (1.16%, 775 ms), target errors (0.46%, 886 ms), and hand&target errors (4.48%, 840 ms). Reaction times between the three error conditions were not significantly different ($F6 = 0.847$, $P = .474$).

For the analysis of lateralized motor activation in association with left and right hand responses, EEG data was analyzed separately for trials with correct hand movements (both correct and target error) and trials with incorrect hand movements (hand error and hand&target error), see Figure 2. The negative LRP shown in blue reflects the relative activation of the hemisphere contralateral to the correct response hand. The positive LRP shown in red shows the relative activation in association with the incorrect response hand. For statistical analysis the mean amplitudes of the LRP in a time window (-356 ms to -16 ms) prior to the offset of the response were calculated. For the correct and incorrect hand responses the means differ significantly ($t6 = -4.926$, $P < 0.003$).

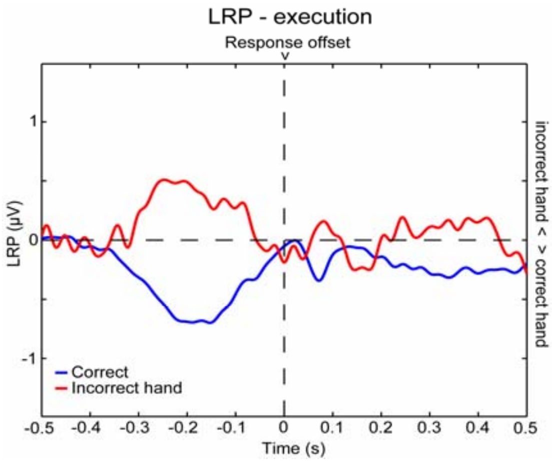

Figure 2. Lateralized readiness potentials for the execution task time locked to the response offset. The blue line shows the LRP for the correct hand responses, and the red line shows the LRP for the incorrect hand responses. Both LRPs were calculated over 7 subjects.

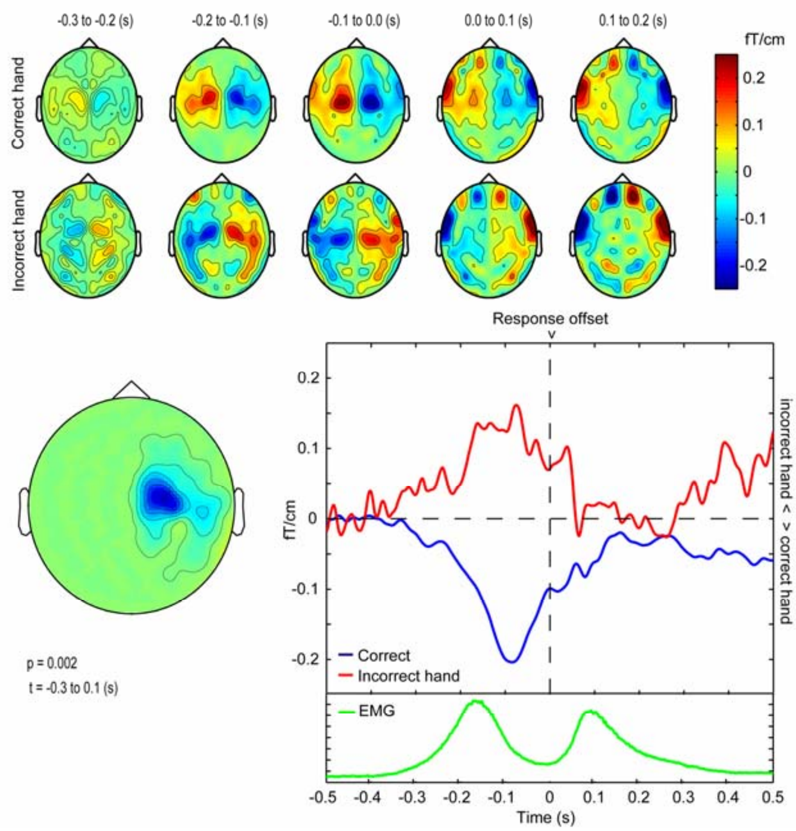

Figure 3. Lateralized readiness fields recorded in the execution task time locked to the response offset. Top, response-locked lateralized readiness fields displayed in topographical plots. The plots range from -0.3 sec. to 0.2 sec., with a time window of 100 ms for each individual plot. The top row of the plots show the topography for correct hand trials, the bottom row shows the topography for the incorrect hand trials. Bottom left, shows the cluster that becomes significant for the comparison between the two conditions (significant between -0.3 and 0.1 seconds). Bottom right, line plot of the LRF for the correct hand actions and incorrect hand actions, derived by averaging the twelve most significant channels. Bottom part of the plot, EMG average for all hand responses

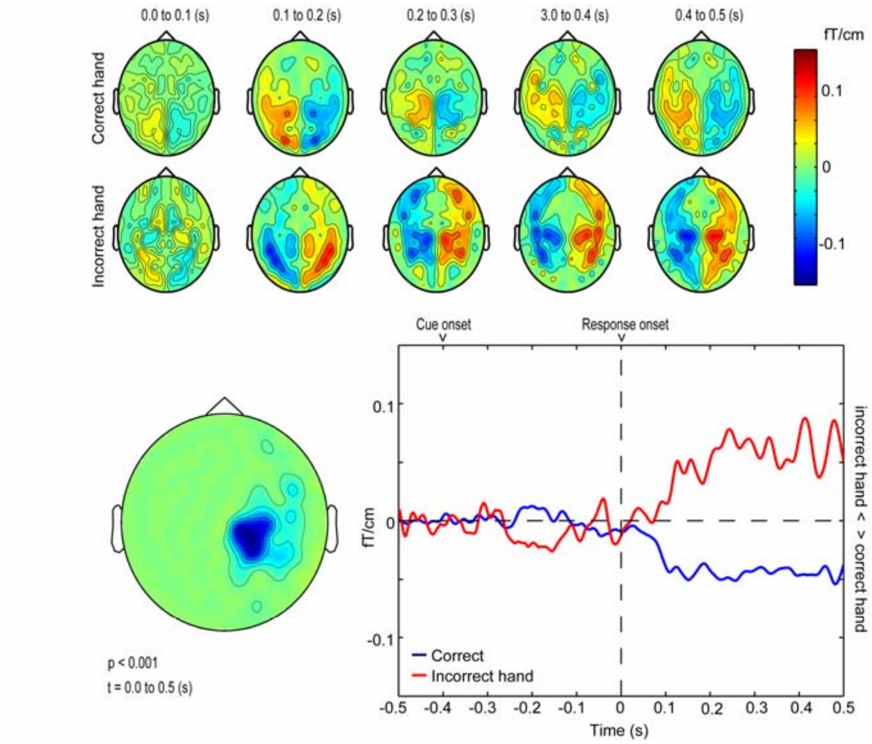

Figure 4. Lateralized readiness fields recorded in the observation task time locked to response onset. Top, response-locked lateralized readiness fields displayed in topographical plots. The plots range from 0.0 sec. to 0.5 sec. with a time window of 100 ms for each individual plot. The top row of the plots show the topography for correct hand trials, the bottom row shows the topography for the incorrect hand trials. Bottom left, shows the cluster that becomes significant for the comparison between the two conditions (significant between 0.0 and 0.5 seconds). Bottom right, line plot of the LRF for the correct hand actions and incorrect hand actions, derived by averaging the twelve most significant channels.

Same procedures were followed for the MEG data with respect to calculating the LRFs for the correct and incorrect hand movements as shown in Figure 3. The top part of Figure 3 shows two rows of topographical distributions of the LRFs ranging from 300 ms prior to the response offset to 200 ms after the response offset. The first row shows the distributions for the correct hand responses, and the second row shows the distribution for the incorrect hand responses. For the correct hand, LRF analysis reveals activation over the motor cortex that is contralateral to the response hand. In this same area and time frame that showed lateralized activation for correct hand responses a cluster with opposite polarity appears for the incorrect hand (Fig. 3, 2nd row). The difference between the two conditions is reflected in the left bottom part of Figure 3 that shows a highly significant cluster in blue located over the motor cortex. In the right bottom of the figure the LRF is presented as the average activation of the twelve most significant channels. The blue line shows the lateralized activation for the correct hand condition over the hemisphere contralateral to the correct hand. The red line shows the relative activation over the opposite hemisphere for the incorrect hand condition as a positivity. The green line in the bottom part shows the average EMG signal for all hand responses.

Observation condition

Figure 4 displays the results for the observation condition in a similar format as for the execution condition in Figure 3. The top part of Figure 4 shows two rows of topographical distributions of the LRFs in a 500 ms interval following the response stimulus. The first row shows the distributions for the observed correct hand responses, and the second row shows the distribution for the observed incorrect hand responses.

For the correct observed hand LRF analysis shows activation that is stronger contralateral to the hand that was used for the response comparable with lateralized effects found with the execution task. In this same area and time frame a cluster with opposite polarity appears for the incorrect observed hand over the motor cortex. The difference between the two conditions is reflected in the left bottom part of the figure that shows a highly significant cluster in blue located over the motor cortex. In the right bottom of the figure a line plot is presented showing the average LRF for the twelve most significant channels. The blue line shows the correct observed hand condition, and the red line shows the incorrect observed hand condition.

Discussion

In this study we used MEG to study the lateralization of motor activation in association with action observation of left and right hand finger movements. The LRF results of the execution task show lateralized activation over the motor cortex in association with the hand that is used during action execution in correspondence with the results of earlier studies (Coles, 1989) that showed lateralization of motor activation using ERPs (van Schie et al., 2004). Comparable with the execution condition, data analysis of the observation task shows lateralized activation over the motor cortex in association with the observation of left and right hand finger movements. Importantly, the finding of opposite lateralized effects to the presentation of incorrect hand movements shows that the observation LRF truly result from action observation, and not in association with the cue.

The significant differences between correct and incorrect hand movements for both the execution and observation tasks are shown as clusters over the motor cortex. These results are in favor of the hypothesis that activation over the left and right motor cortices will lateralize, as a function of the laterality of the observed hand movements.

Even though the results of the execution and the observation task are sufficiently comparable, there are some differences concerning location and timing. Apart from the overlap in topography of lateralized activity during task execution and observation, the lateralized activity seems shifted backwards slightly in the observation condition. One explanation for this difference is that somatosensory cortex is relatively stronger activated than motor cortex in the absence of an executed response, which would be consistent with previous studies that reported somatosensory activation during movement observation (Avikainen et al., 2002; Rossi et al., 2002). Apart from the difference in timing of the LRF between execution and observation conditions that is explained by the different procedures of both conditions, there is also a difference in duration of lateralization. For the execution task the LRF peaks in a narrow time window while for the observation task the LRF is more stretched out. This can be explained by the backwards movement of the index finger observed when turning off the response stimulus 300ms after the onset. This backward movement could evoke a second LRF that adds up to the first, giving the resulting LRF a stretched appearance.

We conclude that the motor cortex is cross activated during the observation of hand movements. The typical crossed organization that is known to underlie motor performance is found to be preserved in action observation. In general this result is consistent with previous reports that have indicated similarity in motor function during the performance and observation of actions. The present findings suggest that even without explicit instructions, the human brain differentiates between observation of left and right hand movements. This ability to represent the left and right hand movements of others separately may provide an important basis for the understanding of other peoples actions where the laterality of movements are considered to be relevant (e.g. in traffic, games, joint action).

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