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Motor-cortical beta oscillations are modulated by correctness of observed action

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Recent research has demonstrated that cortical motor areas are engaged when observing motor actions of others. However, little is known about the possible contribution of the motor system for evaluating the correctness of others' actions. To address this question we designed an MEG experiment in which subjects were executing and observing motor actions with and without errors. In the execution task subjects were asked to make speeded button presses according to instruction cues. During the observation task, they viewed pictures of an actor's hand making button presses which were correct or incorrect according to the cues. Time–frequency representations of the MEG data demonstrated a depression in oscillatory activity in the beta band activity (15–35 Hz) during execution followed by a beta rebound that was stronger for incorrect compared to correct executions. During the observation task, a similar time-course of the beta activity was identified and importantly the modulations were stronger for the observation of incorrect than correct actions. Sources accounting for the difference in beta activity between correct and incorrect actions were localized using a beamforming technique. Both for the execution and observation conditions sources were identified to the dorsal motor areas comprising both primary and pre-motor cortex. Our findings demonstrate that not only is cortical motor activity modulated by action observation, but the modulation increases when the observed action is erroneous. This suggests that the motor system is engaged in evaluating the correctness of the actions of others.

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Introduction

In our daily lives it is important that we are able to interpret the actions of others in order to interact. It has been proposed that the

motor system is crucially involved in coding for other people's movements, gestures and facial expressions. This notion was initially derived from the findings of mirror neurons. These neurons are found in the frontal lobe area F5 of the monkey brain and their activity can be characterized by single unit recordings. They respond when the monkey is performing a given goal directed action but also when the monkey observes others performing the same action (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). This has led to the hypothesis that pre-motor brain areas are involved in encoding and processing the actions of others by activating neuronal representations similar to those engaged had the subject performed the action himself. This notion is supported by multiple human brain imaging studies that demonstrated activity in inferior frontal gyrus (IFG) during various action observation tasks (Binkofski et al., 1999a,b). Additional areas including parietal regions and superior temporal gyrus have been implicated in the processing of others' actions as well (Fogassi et al., 2005; Nishitani and Hari, 2002; Shmuelof and Zohary, 2006) (for review Buccino et al., 2004a). It is debated to what extent the primary motor cortex is a part of the mirror–neuron system; however, it is clear that the primary motor cortex receives strong input from the IFG. Thus activity in the IFG is likely to modulate the functional state of the primary motor cortex. Indeed, the engagement of the motor system during action observation has in multiple studies been demonstrated in humans by probing the excitability of primary motor areas by measuring motor evoked potentials elicited by transcranial magnetic stimulation (TMS) (Fadiga et al., 1995) (for review Fadiga et al., 2005). Electrophysiological studies using electroencephalography (EEG) and magnetoencephalography (MEG) further support the engagement of the motor system in action observation. For instance, it was recently shown that anticipatory readiness potentials over motor cortex could predict the movement onset of others (Kilner et al., 2004). Using MEG it has been shown that oscillatory beta activity (~20 Hz) from the primary motor system generated in

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response to median nerve stimulation is modulated by the observation of human actions (Hari et al., 1998; Jarvelainen et al., 2001; Jarvelainen et al., 2004). Also spontaneous mu and beta activity has been shown to be modulated in a comparable manner during both the execution and the observation of biological human movements (Babiloni et al., 2002; Caetano et al., 2007; Muthukumaraswamy et al., 2006; Oberman et al., 2005). The sources accounting for this modulation were identified to pre-motor and primary sensori-motor areas contralateral to the movement. In conjunction, these studies consistently implicate the extended motor system, including primary motor areas in processing the actions of others. Most of the evidence reviewed above can be explained by a form of ‘low level’ motor resonance, in which the motor system resonates with the kinematic properties of observed actions.

It has been argued that the engagement of the motor system in action understanding goes well beyond motor resonance (Gallese et al., 2004; Kilner et al., 2004; Rizzolatti et al., 2001). From an empirical perspective more research is required to understand how the motor system is engaged in higher level processing such as evaluating the correctness or meaningfulness of a given action. Interestingly, a study from van Schie et al. (2004), designed to investigate error monitoring in the anterior cingulate cortex (ACC) suggested that motor cortical areas may contribute to monitoring the correctness of observed behaviors, indicating a ‘high level’ form of action understanding. The aim of the present study was to further develop insight in the functional mechanisms that allow action understanding and investigate the nature of motor representations that become activated in this process. More specifically we wanted to know if beta modulation originating from dorsal motor areas is in any way sensitive to the correctness of the behavior that is observed. We hypothesized that if motor activation reflected in the beta band is merely a low level form of motor resonance, beta activation should not be expected to differ between correct and incorrect actions. If, on the other hand, modulations of beta activity would be found sensitive to the correctness of observed actions this would suggest involvement with higher forms of action understanding.

Materials and methods

Subjects

12 healthy subjects (3 female, ages between 22 and 33, 6 right-handed) participated in the experiment. All had normal or corrected-to-normal vision and no neurological disorders were reported. Subjects were informed beforehand about the experimental procedure and gave informed consent. The experiment lasted 2 h of which 45 min were used for preparation and practice.

Apparatus

During the experiment the subjects were seated in a 151-sensor axial-gradiometer whole-head MEG system (VSM/CTF Systems, Port Coquitlam, British Columbia, Canada) placed in a magnetically shielded room. To keep track of finger movements during the experiment, corresponding muscle activation was recorded using electromyography (EMG). Bipolar electrodes were placed on both arms over the extensor of the index finger halfway on the dorsal side of the lower arms (*extensor digitorum*). The horizontal and

vertical electrooculograms (EOG) were recorded bipolarly by electrodes located on the outer canthi of both eyes, and a pair of electrodes on the supraorbital and infraorbital ridge of the left eye, respectively. The MEG, EMG and EOG data were acquired simultaneously using a 600 Hz sampling frequency. Two LUMITouch (Photon Control Inc. Baxter, Canada) optical button boxes (one for each hand) were used for detecting the subjects’ responses. The two button boxes were placed adjacently in front of the subject. The subjects’ elbows were supported by cushions to minimize movement of the upper arm in order to prevent movement artifacts. The index fingers of the subjects left and right hands 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. Visual stimuli were projected onto a semi-transparent screen placed at a distance 70 cm from the subjects’ eyes, using a LCD projector. The cue and response stimuli extended $4.7^\circ \times 4.7^\circ$ and respectively $7.3^\circ \times 12.6^\circ$ (see Fig. 1).

Task and stimuli

The experiment consisted 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 therefore these data were not acquired.

In the execution task red/green colored cues (presented for 0.2 s) consisted of a frame with four dots inside (see Fig. 1). The color of the frame would match one dot in the lower and one dot in the upper row. The matching dot in the lower row indicated whether the left or right finger should be used to press the button. The matching dot in the upper row indicated whether the left or right button should be pressed. In the example in Fig. 1, the green frame indicated that the subject must press the right button with his right index finger. Subjects were instructed to respond as quick and accurate as possible. Two seconds following the registration of the button press the next trial started. The eight different combinations of stimuli (based on frame color and dot positions) were presented in equal numbers for a total of 800 trials.

In the observation task blue/yellow colored cues similar to those in the execution task were presented (0.2 s). The color of the frame was always yellow to make the observation task as unambiguous as possible. In the lower part of the screen hands were shown with index fingers appearing ready to perform button presses. After 0.4 s, a picture showed one of the two hands pressing one of the buttons. The hand returned to the starting position 0.3 s later. The next trial started after 2 s. As in the execution task the color of the frame and the dots indicated which finger to move and which button to press. 70% of displayed hand movements were ‘correct responses’. ‘Incorrect responses’ could be of the following three types: ‘hand errors’ (10%) when the wrong index finger went to the correct button, ‘goal errors’ (10%) where the correct index finger went to the wrong button, and ‘hand&goal errors’ (10%) where the wrong index finger went to the wrong button. In 50% of the trials a given finger moved to the contralateral hemifield. Each block started with 8 correct trials, after which the remaining 72 trials in each block were presented in a random order. Subjects were asked to count and report the number of observed errors at the end of a block. The number of errors was the same for each block. Subjects were

Fig. 1. (A) Stimuli and timing of events in the execution task. Participants responded to the onset of a cue stimulus that provided instructions on which finger to move to which action goal. The relevant finger (left/right) and action goal (left/right) were indicated by the two dots that had the same color (green or red) as the surrounding square (green or red). (B) Stimuli and timing of events in the observation task. Subjects were presented with a cue stimulus of which the square color was kept constant during the observation block. In the lower part of the screen two virtual hands were shown continuously in a starting posture. Virtual apparent responses were created by replacing the photograph of the starting posture with a photograph showing an end posture in which one of the hands had moved to press a button. Subjects' task during observation was to detect and count occasional errors.

asked to keep their eyes on the fixation cross and to minimize blinking.

Data analysis

During the execution task the EMG data was used to determine which index finger moved in each trial. This was done by integrating the rectified detrended EMG signal in a time window -0.2 to 0 s prior to the button press. The power of the moving hand had to be at least twice that of the stationary hand; otherwise the trial was discarded. Button presses were used to determine the end position for each action. Preprocessing involved rejection of trials containing eye and jump artifacts, rejection of trials containing ambiguous responses, and baseline correction over a period of 0.7 to 0.5 s prior to the response offset. Preprocessing on the observation task data involved similar steps. For the execution and observations task respectively 20% and 7% of the trials were discarded. After preprocessing, the axial MEG data was converted to planar gradients using linear interpolation with the neighboring sensors (Bastiaansen and Knosche, 2000). The planar field gradient simplifies the interpretation of the sensor-level data because the maximal signal power is located above the source (Hämäläinen et al., 1993).

The time–frequency representations (TFRs) of power $P(t, f_0)$ for a given signal at time (t) and frequency (f_0) were obtained by convolving a Morlet wavelet $w(t, f_0) = A \exp(-t^2/2\sigma_t^2) \exp(i2\pi f_0 t)$ to the signal, $s(t)$:

$$P(t, f_0) = |w(t, f_0) \times s(t)|^2$$

where $\sigma_f = 1/(2\pi\sigma_t)$ and $A = 1/(\sigma_t\sqrt{\pi})^{0.5}$. We chose the “width” of the wavelet ($m = f_0/\sigma_f$) to be 7. The TFRs were calculated for

the individual trials and then averaged. The power calculated in the interval $t = -0.7$ to -0.5 s with respect to the button pushes for the execution and observation task were used as baseline intervals and relative power changes were characterized. This procedure allowed detection of induced oscillatory activity that was not necessarily phase-locked to the stimuli. For the execution condition two groups of sensors with the strongest beta modulation were selected. They were located over the motor cortex (Fig. 2A). The averaged beta activity from these sensors was used in the subsequent statistical testing for both the observation and execution conditions.

A frequency-domain beamformer source reconstruction method, Dynamic Imaging of Coherent Sources (DICS), was used to identify the sources of the beta activity. Note that, for source reconstruction, we used the data from the original axial sensors and not the planar gradient estimate. The DICS technique uses adaptive spatial filters to localize power in the entire brain (Gross et al., 2001; Liljeström et al., 2005). The filter relies on the cross-spectral density matrix that is calculated with respect to the beta depression (execution: $t = -0.5$ – 0 s; observation: $t = 0.1$ – 0.6 s) and rebound intervals (execution: $t = 0.8$ – 1.3 s; observation: $t = 1.0$ – 1.5 s) of the individual trials and then averaged. A multitaper method (Mitra and Pesaran, 1999; Percival and Walden, 1993) was applied as part of the Fourier transformation in 0.5 s time windows using 3 tapers resulting in ± 4 Hz frequency smoothing. The multitaper approach was used since it effectively allows to control the spectral concentration over a desired frequency range. Note that the analysis was done with respect to a frequency of 19 Hz. As a consequence, the ± 4 Hz frequency smoothing resulted in a 15–23 Hz range, the same range used in the other analyses. Cross-spectral density matrices were calculated from the Fourier transformed data following the tapering.

Fig. 2. Beta modulation during action execution. (A) Grand average time–frequency power spectra for correct and incorrect responses. The time–frequency plots reflect average power in 12 sensors (shown in the right plot) over the motor cortex time-locked to the button press ($t=0$ s). Strong modulation was observed in the beta band. Relative power changes with respect to the baseline are shown. (B) Topography of power in the beta band (15–23 Hz) for correct (top) and incorrect (bottom) responses. The temporal developments in beta activation are shown in five consecutive 400 ms time windows. (C) Time-resolved beta power averaged over 12 sensors over the motor cortex. Middle and right panels show activation over respective ipsilateral and contralateral motor areas. The left panel shows the average activation over both hemispheres. A significant difference between correct and incorrect executed actions was found at 1.05–1.3 s.

Multisphere forward models were fitted to individual head shapes identified from the individual MRIs (Huang and Mosher, 1997). The brain volume of each individual subject was discretized to a grid with a 1 cm resolution. Using the cross-spectral density matrices and the forward models, spatial filters were constructed for each grid point. These filters were applied to the Fourier transformed data and the spatial distribution of power was estimated for each condition.

Different conditions were compared by dividing the power values at each grid point yielding the neuronal activity index (NAI) (Van Veen et al., 1997). The individual subjects' source reconstructions were overlaid on his/hers anatomical MRI, and the anatomical and functional data were subsequently spatially normalized to the International Consortium for Brain Mapping template (Montreal Neurological Institute, Montreal, Quebec, Canada; <http://www.bic.mni.mcgill.ca/brainweb>). After spatial normalization, the source reconstructions were averaged across subjects.

Results

Execution task

For the behavioral results, a pairwise t -test on RT of correct (93.8%, 0.76 s) and incorrect (6.2%, 833 ms) responses revealed

no significant effect ($t(11)=1.807$, $p=0.098$). An ANOVA on RT with error type (hand errors: 1.2%, 0.78 s; goal errors: 0.5%, 0.89 s; hand&goal errors: 4.5%, 0.84 s) as a factor revealed no significant effect ($F<1.0$).

Fig. 2A shows the time–frequency representations of relative power of the data in the execution task for a collection of sensors over sensorimotor areas (six per hemisphere; the sensors are presented in the right part in Fig. 2A). The activity in the beta band was depressed during the button press and it was followed by a rebound 0.5 s later. The topography of the activity in the 15–23 Hz beta band showed a depression over motor cortex, which was followed by an increase (Fig. 2B). When focusing on the 15–23 Hz modulations it is clear that the beta depression was not modulated by the correctness of the subjects' actions (Fig. 2C); however, the beta rebound was higher for the incorrect compared to correct actions. A statistical comparison was performed on the average data from the 12 channels over the motor cortex (six per hemisphere) by means of pair-wise t -test between the correct and incorrect condition for a series of 0.050 s increments over a time period of 0.0 to 1.5 s. Time intervals are considered significant with respect to multiple comparisons if three or more consecutive intervals are significant ($p<0.05$) (Fig. 2C). This requirement controls for multiple comparisons with respect to the 300 intervals

(Lange et al., 1999). Using this criterion the conditions differed significantly between 1.05 and 1.3 s. The beta modulation was also compared, using the same channels mentioned earlier, between the six channels contra- and the six channels ipsi-lateral to the movements (Fig. 2C; right panels). A repeated measurements analysis of variance (ANOVA) on the mean power over a single time period of 0.8–1.3 s with laterality (ipsi or contra) and correctness (correct or incorrect) as factors showed a main effect for laterality ($F(1,11)=14.835$, measured standard error (MSE)=0.121, $p<0.005$), a strong trend for correctness ($F(1,11)=3.530$, MSE=0.317, $p=0.087$), and no interaction effect ($F<1$). This means that the beta modulation was strongest contralateral to the movement; however, the lateralized modulation was not significantly affected by correctness.

The sources accounting for the modulation in the beta band during the execution condition are shown in Fig. 3. The modulation of beta band power was characterized by comparing the 15–23 Hz ($19\text{ Hz}\pm 4\text{ Hz}$ smoothing) activity during the interval of increase ($t=0.8\text{--}1.3\text{ s}$) to the interval of decrease ($t=-0.5\text{--}0\text{ s}$) (see Fig. 2C). This was done for the 8 subjects for whom we had structural MRIs. The single-subject anatomical and functional data were aligned to a standard brain and averaged. The strongest modulation in the beta band was observed in BA6 with the largest value in precentral gyrus for both correct and incorrect motor executions (Figs. 3A and B).

Observation task

Fig. 4A shows time–frequency representations of the data in the observation task for a collection of sensors (the same as for the execution task) over sensorimotor areas. The activity in the beta

band (15–23 Hz) was depressed at the onset of the movement ($-0.2\text{--}0.5\text{ s}$) and was then followed by a rebound ($0.7\text{--}1.5\text{ s}$). Note that the magnitude of the beta modulation was much weaker compared to the execution task. The topography of the activity in the 15–23 Hz beta band showed a depression over central and posterior areas followed by a rebound (Fig. 4B). Both the beta depression and rebound were modulated by the correctness of the observed actions (significant depression: $0.45\text{--}0.6\text{ s}$ significant rebound: $1.3\text{--}1.45\text{ s}$, Fig. 4C). The ipsi- and contralateral observed movements were also studied separately (Fig. 4C; right panels). A repeated measurements ANOVA over a time period of $1\text{--}1.5\text{ s}$ with laterality (ipsi or contra) and correctness (correct or incorrect) as factors revealed a significant laterality ($F(1,11)=4.860$, MSE=0.004, $p=0.050$), a significant effect for correctness ($F(1,11)=6.846$, MSE=0.021, $p<0.05$), and no interaction effect ($F<1$). No laterality effect was identified with respect to the beta depression. Thus, the beta rebound was strongest for sensors contralateral to the observed movement; however, there was no interaction effect so a significant modulation of correctness did not result in a stronger laterality. We also compared the differences in beta power with respect to individual error types ('hand', 'goal' and 'hand&goal' errors); however, no statically significant modulations emerged.

The results of source localization on the action observation data are shown in Fig. 5. The modulation of beta band power was derived by comparing the beta band (15–23 Hz) increase ($1\text{--}1.5\text{ s}$) to the decrease ($0.1\text{--}0.6\text{ s}$) (see Fig. 4C). When subjects were observing correct motor responses, beta modulation was primarily localized in superior parietal lobule (BA7) and weakly extended to the dorsal motor areas (Fig. 5A). When the subjects observed erroneous motor responses beta modulation was localized both in the superior parietal

Fig. 3. Source reconstructions accounting for the beta modulation in the execution task. The rebound interval ($0.8\text{--}1.3\text{ s}$) was compared to the beta depression interval ($-0.5\text{--}0\text{ s}$). The source reconstructions were performed for correct (A) and incorrect actions (B). In both cases the strongest beta modulation was identified in the left and right precentral sulcus and adjacent middle frontal cortex. Source activation is projected on a standard brain. NAI refers to the ratio in power with respect to the rebound and depression intervals ($\text{NAI} = (\text{power}_{\text{rebound}} - \text{power}_{\text{depression}}) / \text{power}_{\text{depression}}$).

Fig. 4. Beta modulation during action observation. (A) Grand average time–frequency power spectra for correct and incorrect responses. The time–frequency plots reflect average power in 12 sensors (shown in the right plot) over the motor cortex time-locked to the presentation of the picture indicating the motor action ($t=0$ s). Strong modulation was observed in the beta band. (B) Topography of power in the beta band (15–23 Hz) for correct (top) and incorrect (bottom) responses. The temporal developments in beta activation are shown in five consecutive 0.4 s time windows. (C) Average beta power over time containing data from 12 sensors over the motor cortex. Middle and right panels show activation over respective ipsilateral and contralateral motor areas. The left panel shows the average activation over both hemispheres. A significant difference between observed correct and incorrect actions was found during beta desynchronization (0.45–0.6 s) and during the beta rebound (1.3–1.45 s).

lobule and dorsal motor areas (BA6) with the largest difference in the precentral gyrus (Fig. 5B). When contrasting correct and incorrect observed movements, the difference in beta activity was again localized to the dorsal motor system (BA6); however, the largest difference was in SMA (Fig. 5C).

Discussion

We have here investigated the modulation of oscillatory brain activity in the beta band to improve the understanding of the functional nature of motor activation induced by action observation. Beta activation during execution and observation of goal-directed finger movements revealed the characteristic bi-phasic modulation (Jurkiewicz et al., 2006; Pfurtscheller et al., 1994; Salmelin and Hari, 1994) consistent with earlier studies that have shown similarity between observation and execution of actions in the beta band (e.g. Babiloni et al., 2002; Caetano et al., 2007; Jarvelainen et al., 2004). Our main result is that beta activation in dorsal motor areas during action observation was modulated by the observed action correctness, implicating the influence of higher level evaluative processes. These findings provide convincing support for the hypothesis that the motor system does not merely provide a motor copy for any

movement that is observed, but is sensitive to the correctness of the actions that are displayed. We suggest that this function may be particularly important to support social functions such as observational learning (Flanagan and Johansson, 2003), where the correctness of observed behavior needs to be taken into account.

Previous studies that investigated oscillatory activity in the beta band have functionally distinguished between the two phases of beta modulation (Jurkiewicz et al., 2006; Pfurtscheller et al., 1994). A decrease in beta power is typically considered to be the result of asynchronous neural activation within sensorimotor cortices that accompanies movement preparation and production. The beta rebound or increase in synchrony that accompanies movement termination is generally believed to reflect active inhibition or deactivation of the motor system (Pfurtscheller et al., 2005; Salmelin et al., 1995). While modulations of the beta activity are observed in response to the engagement of the somatosensory and motor system, little is known about the role of the beta rebound in relation to movement errors. We propose that the beta rebound we observe following errors reflects active inhibition of ongoing motor processes: the stronger rebound accompanying the generation of an error reflects response inhibition that typically follows the detection of an erroneous action (Ridderinkhof et al., 2004).

Fig. 5. Source reconstructions accounting for the beta modulation in the observation task. Separate source reconstructions were performed for correct actions, incorrect actions, and the difference in activation between correct and incorrect actions. (A) Beta modulation induced by observed correct actions was mainly found in bilateral superior parietal lobules but it also extended to precentral areas. (B) Beta modulation induced by incorrect actions was strongest in the bilateral superior parietal lobules and in the bilateral precentral sulcus. For both panels A and B the rebound interval (1–1.5 s) was compared to the beta depression interval (0.1–0.6 s) ($NAI = (power_{rebound} - power_{depression}) / power_{depression}$). (C) The difference in beta modulations between incorrect and correct actions was strongest around the precentral gyrus and supplementary motor areas (see Fig. 3). For panel C the rebound interval (1–1.5 s) for correct actions was divided by the beta interval (1–1.5 s) for incorrect actions. Source activation is projected on a standard brain ($NAI = (power_{incorrect} - power_{correct}) / power_{correct}$).

A beamformer analysis was applied to identify the dominant sources accounting for the beta modulations. It should be mentioned that while source modeling is associated with potential inaccuracies due to the inverse problem (Lutkenhoner, 2003), the beamformer technique has been shown to provide sensible results when identifying sources of oscillatory activity (Hillebrand et al., 2005). In the execution condition the beamformer approach revealed sources accounting for the beta modulation in the precentral gyrus in line with previous studies that localized oscillatory beta activity in dorsal motor cortical areas in both monkeys and humans (e.g. Jensen et al., 2005; Salmelin et al., 1995; Sanes and Donoghue, 1993). Given the low number of error trials in the execution condition, we were not able to reliably localize the sources reflecting the difference between errors and correct trials. In the observation condition we identified the dominant sources of beta modulation in the same precentral areas and in the superior parietal lobule. The difference between correct and incorrect observed actions was localized to pre-central areas

including the supplementary motor area. These results suggest that dorsal motor areas were activated both during action execution and during action observation. Importantly, in both conditions, beta oscillations observed at the sensors located over motor cortex were modulated more strongly for errors than for correct actions, suggesting a common functional mechanism to support the processing of self- and other-generated errors. It should be noted that the areas we identified to be modulated by error observation are not part of the 'classical mirror neuron system' as for instance the inferior frontal gyrus (IFG). However, as also argued by Caetano et al. (2007), the identified motor areas are downstream to the IFG. Thus activation of the mirror neuron system in IFG is likely to modulate the beta activity in the dorsal motor system.

Despite of the similarities between the execution and observation conditions, also a few differences in beta modulation were noted. One difference between error-processing in the two conditions was that in the execution condition errors exclusively modulated the magnitude of the beta rebound, whereas in the

observation condition beta modulations were found to enhance both the rebound and the earlier desynchronization phase. A possible explanation for this difference is that error detection in the execution condition may have been delayed relative to the observation condition. In the execution condition errors mostly occurred because subjects misinterpreted the cue (i.e. in 4.5% of the trials subjects followed the wrong color). In the observation condition, on the other hand, cues were less likely to be misinterpreted because the color of the frame was kept constant. As a result, subjects were likely to be better prepared to detect errors in the observation condition than in the execution condition, allowing faster detection.

In an already published study we have analyzed and reported lateralized readiness fields (LRFs) from the same data set as here. The LRFs with respect to observed left and right hand movements revealed that motor areas showed directional tuning in accordance with the laterality of hand movements already after 83 ms (van Schie et al., *in press*). The latency of the error modulation in the beta band is consistent with the hypothesis that motor activation to observed actions may reflect high level action understanding as opposed to a low level automatic motor resonance. In fact, the timing of error modulation in the observation condition (~ 0.5 s) provides ample time for other error processing mechanisms to become activated in advance. In a previous ERP study that investigated error processing during action observation an error-related negativity was found reflecting activation of the anterior cingulate cortex (ACC) already after 0.25 s (van Schie et al., 2004). Hence, it is possible that the modulation in beta oscillations to observed errors in the present experiment were influenced by the outcome of error monitoring in the ACC. Consistent with this suggestion different studies have stressed the link between midline frontal monitoring and sensorimotor networks (Luu and Tucker, 2001).

A prominent difference between the execution and observation conditions is that beta activity was found to originate from bilateral parietal areas in addition to the precentral areas during action observation. This is in line with earlier findings showing activation in the inferior part of the parietal lobes during action observation (Buccino et al., 2004b). In addition Stevens et al. (2000) found the superior parietal lobule activated when subjects were presented with photographs evoking apparent biological motion of the human body. To what extent such activation of superior parietal lobule is related to the modulations of parietal beta oscillations requires studies explicitly addressing this issue.

In conclusion, the present study showed that motor-cortical beta oscillations are modulated by the correctness of observed actions. This finding suggests that the motor system is involved in higher forms of evaluating observed actions. Our result therefore support the frequently conveyed, but ill confirmed notion that the motor system provides a natural basis for understanding and interpreting the actions conveyed by others. We believe that the ability to classify the outcome of other peoples' actions as correct or incorrect provides a crucial element for social forms of imitation learning (Heyes, 2001) and joint action (Sebanz et al., 2006) in which the correctness of observed actions need to be taken into account.

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