A role of beta oscillatory synchrony in biasing response competition?

Beta-range oscillatory activity measured over the motor cortex and beta synchrony between cortex and spinal cord can be up- or downregulated in anticipation of a postural challenge or the initiation of movement. Based on these properties of beta activity in the preparation for future events, the present investigation addressed whether simultaneous up- and downregulation of beta activity might act as an online mechanism to suppress and select competing responses. Measures of local and long-range beta synchrony were obtained from electroencephalographic and electromyographic signals recorded during a cued choice reaction task. Analyses focused on task-related changes in beta synchrony during a 2s delay period between cue and response signal. Analyzed separately, none of the beta measures (spectral power, corticospinal coherence, corticospinal phase synchronization) showed simultaneous up- and downregulation over opposite hemi-spheres controlling the competing responses. However, the combined pattern of beta measures showed beta power desynchronization associated with selection of a response and increased corticospinal coherence and phase synchronization associated with suppression of a response. These results indicate that concurrent up- and down-regulation of different components of beta oscillatory activity is likely to have a functional role in response selection, resembling attentional modulation of alpha activity in visual selection.
3.1 Introduction

Population measures of motor cortex neural activity show a characteristic modulation of oscillatory activity in the beta frequency range preceding and following movement. The modulation consists of an anticipatory decrease and postmovement increase in power. A similar pattern can be observed for the synchronization strength between oscillatory activity in motor cortex and spinal cord, exemplified by high beta-band corticospinal synchrony during steady grip force, which is abolished during movement. This modulation pattern suggested that beta activity is associated with a resting or idling state (Pfurtscheller et al. 1996). Recently, Brown and coworkers provided evidence for an active role of cortical and corticospinal beta synchrony in postural stabilization (Gilbertson et al. 2005; Androulidakis et al. 2007), indicating that changes in beta activity are causally relevant and not merely epiphenomenal. Key for the proposed role is an anticipatory upregulation of beta activity prior to an expected postural challenge, contrasted with the traditionally reported down-regulation of beta activity before a speeded motor response. Related evidence for an association between beta synchronization and response inhibition was reported in an inhibition-of-return task (Pastötter et al. 2008). Building on the existing evidence that beta activity can be prospectively increased or decreased in a task-relevant way, we investigated whether beta activity in neural populations implementing competing response alternatives is modulated to bias response competition in favor of the selected response. A role of beta activity in suppressing and facilitating competing response alternatives would resemble the regulation of alpha activity in visual attention. Attending selectively to left or right hemispace is suggested to involve antagonistic suppression and enhancement of alpha activity over the occipital cortex contralateral to the attended and nonattended side (Worden et al. 2000; Rihs et al. 2007).

Relevant physiological measures were extracted from electroencephalographic and electromyographic data (EEG and EMG, respectively) recorded in a cued choice reaction task, in which a cue provided information as to which hand to prepare for an upcoming response. This instruction cue was followed at a fixed interval by an imperative signal indicating the response hand. Within the interval between cue and response signal (referred to as delay period), we were interested in early and late effects, representative of selection and preparation processes, respectively. Regarding response selection, there is already evidence for opposing influences on neural excitability of left and right hemisphere motor cortex from movement-related potential studies (Vidal et al. 2003; Praamstra and Seiss 2005) and from transcranial magnetic stimulation (Leocani et al. 2000; van den Hurk et al. 2007), but is there also a role of oscillatory synchrony in the selective facilitation and inhibition of competing...
responses? As to response preparation, it is known already that the premovement decrease in beta activity shows hemispheric lateralization as a function of the cued hand in a cued choice reaction task (Doyle et al. 2005; Kilner et al. 2005), but is there a corresponding lateralization of corticospinal synchronization? Based on the work of Androulidakis et al. (2007) and on the modulation of corticospinal coherence by response readiness (Schoffelen et al. 2005), we expected differential beta power and corticospinal synchronization effects for the selected and nonselected response in appropriate time windows for response selection and response preparation.

### 3.2 Methods

**Participants**

Fifteen healthy volunteers participated in the experiment (nine male, age 29 ± 8 years). Three participants were left-handed and one ambidextrous according to the Edinburgh Handedness Inventory (Oldfield 1971). Data of two participants were excluded because of excessive noise in their EEG recording and substantial loss of trials due to incorrect behavioral responses. Two further participants were excluded because their data did not display significant corticospinal synchronization in any condition. All participants gave written informed consent and were paid for their participation. The research was approved by the local ethics committee.

**Behavioral task and stimuli**

The task was a cued choice response task, adapted to measuring corticospinal synchronization by the use of compliant rubber bulbs as response force measurement devices, one for each hand. Because the focus of interest was on the modulation of cortical and corticospinal synchronization during the selection and preparation of a manual response, participants maintained a constant, instructed force during the presentation of the cue stimulus and the following fore period between cue and response signal. Participants initiated a trial by increasing left and right hand force levels to the target force range (see Figure 3.1). When both force levels had stayed within target range for 2s, the cue stimulus (S1) was displayed, consisting of arrows pointing either to the left or to the right. Participants had to maintain the same force level for another 2s with both hands, after which a response stimulus (S2) was displayed, again consisting of arrows pointing either left or right. Participants were asked to respond by increasing the force level of the response hand as quickly as possible while maintaining the same force level with the nonresponse hand. After the
Figure 3.1. Experimental set-up of a trial. Left panel shows example force profiles of the response hand (solid line) and nonresponse hand (dashed line) during a trial. Right panel resembles a screen shot during a trial. Note that in the experiment, stimuli were presented in white against a gray background and force feedback was displayed by color-changing bars.

response, grip of both hands was released and participants could initiate the next trial in their own time.

The experiment consisted of eight blocks of 60 trials each (30 left hand responses, 30 right hand responses). In four blocks constituting the predictive cue condition, the cue information was 100% valid regarding the side of the response, that is, the cue direction was always identical to the direction indicated by the response signal. In the remaining four blocks (the nonpredictive cue condition) cue validity was 50%, rendering the cue direction nonpredictive for the response side. Predictive cue and nonpredictive cue blocks were arranged so that two successive blocks were of the same type, with their order counterbalanced across subjects. Prior to each block, participants were informed whether S1 was predictive with respect to the upcoming response or not. Right and left hand responses were randomized within each block.

The experiment was run in a normally illuminated room with participants comfortably seated in a chair with their 90° pronated forearms leaning on the armrests. The compliant rubber bulb (Ø 4 cm) response device was held between thumb and index finger and supported by the middle finger. Force was exerted by squeezing the bulb. Visual stimuli were presented in white against a gray background on a computer screen at 100 cm distance. Participants were instructed to center their gaze on a 1.4° × 1.4° fixation area in the center of the screen surrounded by brackets (see Figure 3.1). Cue and response signals were presented within that area and measured 0.7° × 0.7° of visual angle with a display duration of 200 ms. Online feedback about left and right hand force levels was provided by means of two colored bars (combined size 0.9° × 3.6° directly below the fixation area. With increasing force level, the height of the bar increased and its color changed from green to red. Target force level (~1N) and range (~ ±0.2N) were marked on the two bars. Participants
were instructed to monitor the produced force level while they built up force, but maintain their center of gaze onto the fixation area. Participants could rest between blocks and relax their fingers. Before recordings participants performed a practice block to familiarize themselves with equipment and task.

**Instrumentation and physiological recordings**

Experimental control of stimulus presentation was performed via custom written software. Measurement of force levels was realized via air pressure variation in two closed pneumatic systems, each consisting of a compliant rubber bulb connected by 2m length of 2-mm ID tube to a piezo resistive pressure sensor (Honeywell 40PC015G1A). The pressure sensor output signal was fed through the EEG AD-converter and stored with EEG and EMG signals. For online feedback, the sensor output was AD-converted by a National instruments NI-PCI-MIO-16E board at the screen refresh rate (100 Hz). Calibration of the system was performed periodically between experiments using a secondary precision load cell. EEG was recorded with Ag/AgCl electrodes from 128 scalp electrodes, including left and right mastoid electrodes. A nylon cap was used to place the electrodes according to the 10-5 electrode system (Oostenveld and Praamstra 2001). Concurrently, surface EMGs were recorded above the first dorsal interosseous muscle and flexor pollicis brevis muscle of both hands, with electrodes placed on the muscle belly and tendon. All signals were low-pass filtered (cut-off frequency at 256 Hz) and amplified before sampling at a rate of 1024 Hz (BioSemi Active-Two amplifiers).

**Behavioral responses**

Reaction times and response accuracy were determined using the continuous force recordings. The baseline force level was defined as the mean force in the time window from -1000 ms until the onset of the cue signal (S1). Reaction time was defined as the time point after the response signal (S2) at which the force of the correct response hand exceeded a threshold of 105% of the baseline force. Responses were classified incorrect if the force level of a hand exceeded a threshold of 110% of the baseline force during the fore period between S1 and S2, if the force level of the nonresponse hand exceeded 105% baseline force level during the response interval, or if the latter dropped below 95% baseline force level before 350 ms after S2. All incorrect trials were removed before analysis of response times and left out from the EEG analyses. The response times were statistically evaluated with a repeated measures ANOVA with factors cue information (predictive vs. nonpredictive) and hand (left vs. right).
Movement-related potentials

After removal of incorrect responses and exclusion of artifact contaminated EEG segments, there remained >96 trials per condition for each subject for EEG/EMG analyses. For extraction of movement-related potentials, EEG was analyzed using BrainVision Analyzer software (Brain Products GmbH, Germany). The continuously recorded data were referenced to off-line averaged mastoid electrodes and then segmented into epochs of 3.5s, that is, from 500 ms before S1 to 1000 ms after S2. Epochs were averaged separately for each of the four conditions, with a 500 ms prestimulus baseline. To evaluate whether participants used cue information, lateralized movement-related potentials were derived by computing difference potentials between homologous electrode sites over left and right hemisphere. That is, EEG at channels ipsilateral to the cued response hand was subtracted from the signal recorded at contralateral sites. Subsequently, averaging over left and right hand conditions yielded lateralized movement-related potentials, which were computed separately for the predictive and nonpredictive cue condition. In the nonpredictive condition, lateralized potentials were also calculated relative to the actual instead of the cued response side. The lateralized potentials of interest were the anterior directing-attention negativity (ADAN) associated with the selection of a response (Verleger et al. 2000; Praamstra et al. 2005), and the lateralized readiness potential (LRP) associated with preparation and execution of a response (Leuthold et al. 1996). ADAN and LRP were quantified in a time window from 400 to 450 ms and 1800 to 2000 ms after S1, respectively, in a selection of channels corresponding to the scalp maximum (ADAN: FCC3h/4h, FCC5h/6h, FC3/4, FFC3h/4h and FFC5h/6h; LRP: C1/2, C3/4, CCP3h/4h, and FCC3h/4h). For the purpose of topographic mapping using spherical spline interpolation (Perrin et al. 1989), the lateralized potentials were displayed in antisymmetric fashion over both sides of the head (cf. Praamstra et al. 1996). For the statistical evaluation of movement-related potentials we used paired-samples t-tests.

Time-frequency analysis

For time-frequency analyses, data were preprocessed in BESA (Brain Electrical Source Analysis, MEGIS Software GmbH, Germany) to create reference-free current source density derivations (Perrin et al. 1989) optimal for analysis of corticospinal synchronization (Mima and Hallett 1999). Both EEG and EMG signals were band-pass filtered (bidirectional fourth-order Butterworth filter, 5-150 Hz), and resampled to 512 Hz to optimize computation time and storage space.

Time-frequency analyses were performed in Matlab (ver 7.4, MathWorks, Natwick, MA). We used the open-source FieldTrip toolbox (www.ru.nl/fcdonders/fieldtrip) for
the calculation of spectral power and coherence. All data were segmented into epochs of 4.5s, starting 2000 ms before S1 and ending 500 ms after S2. After DC-removal, EMG data were rectified via the analytical signal constructed using the Hilbert transform (Myers et al. 2003). Time-frequency spectra for EEG and rectified EMG were calculated using a multitaper method with Slepian sequences based tapers. This involved the use of a sliding window with time steps of 50 ms and 2 Hz frequency bins from 5 to 69 Hz. Per frequency bin the window length was chosen as five periods of the central frequency, that is, $5/frequency$. We further applied a spectral smoothing of $\pm 0.4 \times frequency$, which resulted in three tapers per window. All power spectra were log-transformed before averaging to improve normality (Halliday et al. 1995). The beta-band turned out to display the most pronounced task-related modulations throughout analyses (see Results). Hence, we selected the frequency range 15-30 Hz and averaged the power spectra over these frequencies. EEG power spectra were averaged across four channels overlying the left motor cortex (C1, C3, CCP3h, FCC3h) and across the homologous right hemisphere channels (C2, C4, CCP4h, FCC4h).

We adopted the approach of Baker and Baker (2003) for the calculation of time-frequency cross-spectra between each muscle and all EEG channels. Absolute coherence values were Z-transformed and corrected for a possible bias by subtracting the mean coherence over all time points within a frequency range in which significant coherence was absent during the whole epoch. Subsequently, Z-values were averaged over the two muscles per hand, the previously selected EEG channels (see above) and over the 15-30 Hz frequency band. All values were related to a significance level as defined in Rosenberg et al. (1989). As mentioned earlier, two participants who did not display significant coherence were excluded from further analysis.

For the analysis of corticospinal phase synchronization, defined as the phase uniformity of the relative phase between EMG and EEG signals (Mardia and Jupp 2000; see also Mormann et al. 2000 for application), we used consecutive 2 Hz frequency bins from 5 to 69 Hz (overlapping by 1 Hz). Per frequency bin the raw signals were filtered (bidirectional second-order Butterworth) and the analytical signal, calculated via the Hilbert transform, yielded the Hilbert-phase at every instant. Phase uniformity was calculated as mean resultant length of the difference between the phase of the EMG and EEG signals. Equivalent to coherence, the uniformity values were averaged over the two muscles per hand, over the earlier selected EEG channels and across the 15-30 Hz frequency band. Prior to averaging we applied Fisher’s transform, atanh, and used tanh to invert the transform of the means (Amjad et al. 1997).

In order to correct for inter- and intra-individual differences in absolute values, the power and phase synchronization values were divided by the corresponding mean values estimated in the baseline interval -500 to 0 ms. Subsequently, power,
coherence and phase synchronization measures were averaged across left and right hand conditions, to express them in terms of the hemisphere contralateral and ipsilateral to the cue direction. Mean absolute values averaged over left and right hand trials did not differ between conditions in the baseline interval as determined with paired-samples t-tests. Results were statistically evaluated with 2 × 2 repeated measures ANOVAs with factors cue information (predictive vs. nonpredictive) and hemisphere (ipsi- vs. contralateral to cued hand). Separate ANOVAs were performed on time windows 200-1000 ms and 1500-2000 ms, selected on the basis of visual inspection of the data. In addition, data points in the 200- to 1000-ms interval were compared with the baseline interval using serial two-tailed paired t-tests, yielding time-evolving p-values. In order to correct for type I errors due to the large number of comparisons (17), we considered effects to be significant only when p-values of at least two consecutive data points were below .05 (see Lange et al. 1999).

3.3 Results

Response times

Participants responded significantly faster in trials with predictive cues (307 ± 53 ms) compared with trials with nonpredictive cues (421 ± 36 ms), expressed in a significant main effect of cue information ($F_{1,10} = 190.07$, $p < .001$). There was no effect of hand ($F_{1,10} < 1$) and no interaction effect ($F_{1,10} < 1$). In the nonpredictive cue condition, reaction times were not significantly different ($F_{1,10} = 1.53$, $p = .156$) between trials with congruent cues (426 ± 54 ms) and trials with incongruent cues (415 ± 54 ms). In view of the number of non-right-handed participants, analyses were also performed in terms of dominant versus nondominant hand, instead of right versus left, yielding comparable results.

Movement-related potentials

The analysis of response times demonstrates that participants benefited from predictive cues relative to nonpredictive cues. We analyzed movement-related potentials to establish whether this response time benefit was associated with advance preparation during the fore period. Movement preparatory activity was found in the form of the ADAN and the LRP, represented in Figure panels 3.2a,b, respectively. The ADAN is generally elicited by directional information guiding the direction of spatial attention or the side of a manual response. It is typically distributed over the frontocentral scalp, peaking at about 400 ms. Accordingly, the present data displayed an ADAN peaking at 425 ms after the cue with an appropriate
distribution. The amplitude was significantly different from zero, both in the predictive and in the nonpredictive cue condition ($t(10) = 4.31, p = .002$ and $t(10) = 3.61, p = .005$, respectively). Although higher in the former compared with the latter, this difference was not significant ($t(10) < 1$). When lateralized potentials in the nonpredictive cue condition were computed relative to the response side instead of the cue direction, the ADAN effects of left and right directed cues cancelled each other, eliminating the ADAN.

**Figure 3.2.** Time course and scalp distribution of the lateralized potentials. **A)** ADAN. **B)** LRP. Amplitudes are averaged over the selected channels marked with a +. Solid line: predictive cue condition, dashed-dotted line: nonpredictive cue condition, dashed line: nonpredictive cue condition with respect to response side. The gray bars indicate the time intervals used for statistical evaluation and for display of the scalp distributions. The scalp distribution of the ADAN is averaged across the predictive and nonpredictive cue condition. The LRP scalp distribution represents the predictive cue condition only.
Results for the LRP are shown in Figure 3.2b. The scalp topography showed a more posterior distribution of lateralized activity compared with the ADAN. The slowly rising negativity before the response signal in the predictive cue condition is related to response preparation and was significantly different from the signal recorded for the nonpredictive cue condition. This was the case when the LRP of the latter condition was computed relative to the cue direction \((t(10) = 3.62, p = .005)\) and when calculated relative to the response side \((t(10) = 3.38, p = .007)\). Hence, faster response times in the predictive cue condition were accompanied by preparatory activity that was lateralized to the hemisphere contralateral to the cued response side before onset of the response signal. In summary, these results demonstrate that the task of maintaining a constant force level during the delay period did not prevent subjects to exploit the cue information for the advance selection and preparation of a response.

**Time-frequency analyses**

Time-frequency analyses started with determining the time-frequency windows and corresponding scalp distributions of task-related changes in synchronized activity, which were concentrated in the beta-range (see Figure 3.3a). The beta cortical power modulations showed a frontocentral scalp distribution, as illustrated in Figure 3.3b. The figure represents the preparatory decrease in power (desynchronization) in the final 500 ms of the delay period. This decrease in power was lateralized to the hemisphere contralateral to the prepared response side in the predictive cue condition, but had a midline focus in the nonpredictive cue condition. The scalp channels overlying the lateralized maxima also appeared to be the four channels with the strongest corticospinal synchronization (Figure 3.3b). These two groups of channels were therefore selected for further analyses of beta power modulation, corticospinal coherence and phase synchronization.

All measures of beta activity (15-30 Hz) were averaged across the four channels and their time courses were plotted separately for hemispheres contra- and ipsilateral to the response side (see Figure 3.4). Power, coherence, and phase synchronization increased during the first part of the trial when participants increased grip force from zero into the target force range and reached a plateau at -500 to 0 ms serving as baseline interval. Differences between hemispheres and conditions were found in the interval between S1 and S2, which will be described below. Differences in the final 1000 ms were assumed to be related to response preparation, as already signaled by a steep reduction in beta activity during this time window. They were attributed to the processing of cue information and response selection in the first 1000 ms of the delay period.
Figure 3.3. A) Time-frequency representation of corticospinal coherence between the left first dorsal interosseous muscle and selected EEG channels (see B) overlying the contralateral motor cortex. The frequency band selected for analysis (15-30 Hz) stands out as the frequency band with strongest coherence. Shown here are grandaveraged data for the predictive cue condition with left hand responses. Corticospinal coherence for the left flexor pollicis brevis muscle and the 2 muscles of the right hand, as well as corticospinal phase synchronization, were confined to the same frequency range in all conditions. B) Scalp distribution of EEG beta power and corticospinal coherence. Top row shows the laterialized distribution of EEG power (15-30 Hz) during the preparation for a left (left) and right hand response (right) in the predictive cue condition (time window 1500-2000 ms). Power values were divided by the average power in the baseline interval and averaged over participants. Channels marked with a + were selected for analysis. Bottom row shows the scalp distribution of corticospinal coherence (15-30 Hz) for the first dorsal interosseous muscle of the left and right hand (left and right panel, respectively) in the predictive cue condition with left hand responses. Coherence was localized over the motor cortex with an expansion over fronto-medial channels. Scalp distributions for corticospinal phase synchronization were similar.
Figure 3.4. Time course of EEG power, corticospinal coherence and corticospinal phase synchronization. The time series represent values averaged over left and right hand trials, selected channels, beta frequency band (15-30 Hz) and participants and are divided by the mean of the baseline line interval. Analyzed time windows are indicated with gray bars. Note the similar time course for the different measures as well as the absence of the short-lasting amplitude drop around 500 ms for phase synchronization. Data points in the 200-1000 ms interval that differed significantly from baseline are indicated with black lines above (for the ipsilateral hemisphere) and below (for the contralateral hemisphere) the gray bars.
Early delay period effects

Effects in the first 1000 ms of the fore period were not straightforward to characterize due to multiple phases of beta power decreases and increases (see Figure 3.4). Ignoring these multiple phases, that is, comparing beta power between conditions across the entire 200-1000 ms window, we found a significant main effect of hemisphere due to lower beta power contra- than ipsilateral to the cue direction. In addition, there was lower beta power in the predictive than in the nonpredictive cue condition as expressed in a significant main effect of cue information (see Table 3.1). The hemispheric difference in power being stronger in the predictive than in the nonpredictive cue condition yielded a significant interaction of hemisphere by cue information. Serial two-tailed paired t-tests were conducted to compare power in the interval 200-1000 ms to baseline. As shown in Figure 3.4, power for the hemisphere contralateral to the cued hand in the predictive cue condition decreased significantly, whereas in the nonpredictive cue condition there were brief periods of significant increases.

Corticospinal coherence in the early 200-1000 ms interval followed the same time course as beta power (see Figure 3.4) and demonstrated the same pattern of effects, except for a nonsignificant interaction of cue information by hemisphere (see Table 3.1). This similarity between beta power and betarange corticospinal coherence was not entirely unexpected given that coherence estimates may be influenced by amplitude. Phase synchronization, by contrast, is by construction independent of amplitude. Figure 3.4 reveals that the most conspicuous difference between coherence and phase synchronization was the absence of the short-lasting amplitude drop around 500 ms, which also characterized the beta power time course. Instead, phase synchronization showed more sustained effects in the 200-1000 ms interval. Similar to coherence, phase synchronization stayed level for the hemisphere contralateral to the cued hand in the predictive cue condition, whereas it increased over the ipsilateral hemisphere, and increased more prominently when cue information was not predictive (see Figure 3.4). This resulted in significant main effects of cue information and hemisphere, again without a significant interaction effect. The more sustained nature of phase synchronization effects was also evident from the sustained significant increase in the serial t-tests compared with baseline in the nonpredictive cue condition, where power and coherence demonstrated significant increases only around peak values. A similar sustained increase of phase synchronization was evident over the ipsilateral hemisphere in the predictive cue condition, although the window in which it reached significance relative to baseline was relatively short (see Figure 3.4).

In summary, across the different measures of beta activity quantified in the 200-1000 ms window, there were instances of beta upregulation and beta down-
regulation. For none of the different beta measures, there was simultaneous up- and
downregulation of activity over the hemispheres controlling the noncued and the cued
response. Note, however, that in contrast to the later response preparation time
window (see below), cue direction induced an interhemispheric lateralization also
when it was nonpredictive. The interhemispheric lateralization signals that cue
information, though irrelevant in the nonpredictive condition, was processed
nonetheless and affected the motor system. The sustained increase of beta power in
the nonpredictive relative to the predictive cue condition, across the 200-1000 ms
interval, may reflect an upregulation of beta activity to prevent the cue information
leading to differential preparation of left and right hand. Similarly, the increased beta
phase synchronization, over both hemispheres in the nonpredictive cue condition and
over the ipsilateral hemisphere in the predictive cue condition, ‘locks’ the existing
motor state to suppress a response from either hemisphere in the nonpredictive, and
from the nonprimed hemisphere in the predictive cue condition.

Late delay period effects
Response preparation effects in the late interval were straightforward, with a more
pronounced beta desynchronization over the hemisphere contralateral to the cued
response side in the predictive cue condition. This lateralization was not observed
when subjects could not prepare their response in the nonpredictive cue condition.
Together this yielded significant main effects of cue information and hemisphere, as
well as a significant interaction (see Table 3.1). Like beta spectral power, the
coherence and phase synchronization also decreased steeply in the late interval, with
a lateralization only in the predictive cue condition. Again, this was reflected in
significant main effects of cue information and hemisphere as well as a significant
interaction for both synchronization measures (see Table 3.1).

Evidently, the steep reduction in beta power, coherence, and phase synchro-
nization in the second half of the fore period was modulated by cue information, but
not conditional on hand-specific response preparation. Were there, superimposed on
this bihemispheric reduction, signs of antagonistic enhancement and suppression of
beta activity over the hemispheres controlling the nonselected and the selected
response in the predictive cue condition? If so, this would be manifested in higher
(lower) values of beta activity contralateral to the nonselected (selected) response,
relative to the nonpredictive cue condition. Post hoc t-tests indicated that for each of
the beta measures there were significantly lower values over the hemisphere
controlling the selected response, relative to the nonpredictive cue condition. However, there was no significant enhancement of beta activity contralateral to the
nonselected response. Hence, in this late time window, our data did not support an inhibitory role of beta activity.

| **Table 3.1.** Results of the 2 × 2 repeated measures ANOVAs for EEG power, corticospinal coherence and phase synchronization. |
|---|---|---|---|
| Time interval | 200-1000 ms | 1500-2000 ms |
| **EEG power** | | | |
| Cue information | $F(1,10) = 17.28$ | $p = .002$ | $F(1,10) = 7.95$ | $p = .018$ |
| Hemisphere | $F(1,10) = 13.71$ | $p = .004$ | $F(1,10) = 17.99$ | $p = .002$ |
| Interaction | $F(1,10) = 7.17$ | $p = .023$ | $F(1,10) = 17.68$ | $p = .002$ |
| **Corticospinal coherence** | | | |
| Cue information | $F(1,10) = 9.67$ | $p = .011$ | $F(1,10) = 10.16$ | $p = .010$ |
| Hemisphere | $F(1,10) = 5.46$ | $p = .042$ | $F(1,10) = 16.12$ | $p = .003$ |
| Interaction | $F(1,10) = 0.14$ | $p = .717$ | $F(1,10) = 13.66$ | $p = .004$ |
| **Phase synchronization** | | | |
| Cue information | $F(1,10) = 7.73$ | $p = .020$ | $F(1,10) = 6.06$ | $p = .034$ |
| Hemisphere | $F(1,10) = 7.97$ | $p = .018$ | $F(1,10) = 5.04$ | $p = .049$ |
| Interaction | $F(1,10) = 0.16$ | $p = .700$ | $F(1,10) = 7.11$ | $p = .024$ |

Significant effects are indicated in bold.

### 3.4 Discussion

Although the initiation of a new movement is known to be preceded by a down-regulation of beta activity, recent work has demonstrated that beta oscillatory synchrony can be prospectively upregulated when the task requires maintained posture (Gilbertson et al. 2005; Androulidakis et al. 2007). This suggests a mechanistic role of beta synchrony in optimizing the motor state for current tasks. In the domain of visual spatial attention there is evidence for prospective up- and downregulation of activity in the alpha frequency band. Moreover, concurrent up- and downregulation of alpha oscillatory synchrony is suggested to suppress nonattended and facilitate attended input to opposite hemispheres (Worden et al. 2000; Thut et al. 2006). Both these examples concern *anticipatory* adjustments of oscillatory activity for future events. The present investigation addressed whether concurrent up- and down-
regulation of beta synchrony acts as an *online* mechanism implementing the selection between competing motor responses.

We examined both local synchrony and long-range synchrony in the form of corticospinal coherence and phase synchronization. Preparatory processes during the second half of the fore period between cue and imperative signal were associated with a steep reduction of beta synchrony. At the same time, there was a differential modulation of ipsi- and contralateral hemisphere when there was advance information regarding the response side. The contralaterally dominant reduction of beta power replicates earlier work (Leocani et al. 2001; Doyle et al. 2005). The current data, however, are the first to show that not only beta power but also corticospinal coherence and phase synchronization in the same time window differentiate between the hemisphere that is involved and the one that is not involved in the preparation of a response. Schoffelen et al. (2007) did not find such a modulation of corticospinal coherence, possibly due to task differences, in particular a variable S1-S2 timing, and because these authors did not apply a time-resolved frequency analysis. Although our data in the late time window show clear-cut hemispheric differences when participants could prepare a response, both in local and in long-range beta synchrony, the differential modulation does not amount to concurrent up and downregulation. However, it is still conceivable that there is such a modulation in opposite directions, but that it is masked by simultaneous reduction of beta synchrony related to other processes, such as stimulus anticipation and temporal preparation (Praamstra et al. 2006; Alegre et al. 2006). This possibility is difficult to substantiate because there are also known interhemispheric cross-talk effects (Kilner et al. 2003).

Support for a role of beta synchrony in the selection and suppression of competing responses is suggested by the behavior of beta activity in the first half of the fore period. Based on the combined evaluation of power, coherence, and phase synchronization, we hypothesize that beta activity is subject to a relatively sustained condition-dependent modulation that is overlapped by a stimulus-induced beta desynchronization of shorter duration, thus accounting for the multiple phases of beta synchrony increases and decreases in power and coherence in this time window. The stimulus-induced desynchronization is by and large identical between conditions and hemispheres and peaks at about 500 ms, whereas the more sustained modulation is affected by the experimental manipulations and extends from shortly after stimulus onset to about 1000 ms. Because coherence estimates depend on power, it is unsurprising that the stimulus-induced beta desynchronization affected corticospinal coherence (see Figure 3.4). In contrast, power does not influence corticospinal phase synchronization. Thus, the behavior of beta-range corticospinal phase synchronization captures an important part of the observed modulation of local beta synchrony, uncontaminated by the stimulus-induced influence on beta power. Crucially, it reveals
increases of beta synchrony over both hemispheres in the nonpredictive cue condition and over the ipsilateral hemisphere in the predictive cue condition. These increases are plausibly construed as stabilizing the current motor state and inhibiting a motor response from the involved hemispheres. A beta increase related to response inhibition has been shown before in nogo response suppression (Alegre et al. 2004; Kuhn et al. 2004) and, recently, in an inhibition-of-return paradigm (Pastötter et al. 2008) suggesting a possible role in response selection.

In the proposed interpretation, selection of the cued response and deselection of the noncued response are reflected in decreased spectral power and increased phase synchronization, respectively, in opposite hemispheres. A selective decrease of spectral power over the hemisphere controlling the response hand can obviously not be accounted for in terms of the condition-independent stimulus-induced beta desynchronization phase referred to above. That there is another factor that drives beta power down over the hemisphere that is primed for a forthcoming response is suggested by the finding that the ipsilateral-contralateral hemisphere difference in power was more pronounced in the predictive than in the nonpredictive cue condition (expressed in a significant cue information by hemisphere interaction), whereas the interhemispheric difference in phase synchronization was identical between predictive and nonpredictive cue conditions. This supports the antagonistic modulation of beta spectral power and phase synchronization in opposite hemispheres. The possibility of a dissociation between local synchronization and corticospinal synchronization has been established by pharmacological manipulations and by the behavior of beta rhythms in some disease states (Baker and Baker 2003; Riddle et al. 2004; Jensen et al. 2005). In the present context of response selection, the downregulation of cortical and upregulation of corticospinal beta-range synchronization might well represent a means of biasing the competition between alternative, simultaneously activated responses. In van Wijk et al. (2008), we have analyzed the present data from a different perspective, asking whether observed beta spectral power can be explained by a linear superposition of the sustained condition-dependent beta phase synchronization, as one component, and the overlapping, condition-independent stimulus-related beta desynchronization phase, as second component. Using principal component analysis, such a two-component model explains the data remarkably well, except for the beta power reduction in the predictive cue condition over the primed hemisphere. This supports our view that phase synchronization and beta spectral power in opposite hemispheres can be modulated in an antagonistic way, acting together to suppress and select competing responses.

Previous studies of beta oscillatory activity in S1-S2 tasks have also described beta desynchronization and synchronization effects following the cue, both at scalp EEG
level and for local field potentials in the subthalamic nucleus and thalamus (Doyle et al. 2005; Alegre et al. 2006; Klostermann et al. 2007). However, systematic early effects related to the meaning of the cue have, to our knowledge, only been reported in local field potential beta activity recorded from deep brain stimulation electrodes in the subthalamic nucleus in Parkinson’s disease patients (Williams et al. 2003). Of relevance to our findings, the effects were also modulated by the predictive value of cues, though not by cue direction, and inferred to be related to the behavioral exploitation of cue information. Although reports of such early effects are rare, the effects are not entirely unexpected, not even in the situation where the cue information is not task-relevant, as in the nonpredictive cue information condition. For instance, arrow cues carrying no predictive or response-relevant directional information still produce an early lateralization of movement-related activity in the form of the ADAN or LRP components (Eimer 1995; Verleger et al. 2000), as they did here. As to oscillatory activity, beta activity is already known to be modulated by imagined and observed movements, commonly interpreted in terms of a covert motor command (Muthukumaraswamy and Johnson 2004; Caetano et al. 2007; Tkach et al. 2007). Our data indicate that a similar modulation of beta activity is elicited by overlearned symbolic information in the form of an arrow. Significantly, the prospective upregulation of corticospinal coherence in anticipation of a postural challenge, reported by Androulidakis et al. (2007), also occurred in a time window closer to the cue than to the perturbation, suggesting that it (partly) reflected a covert motor command elicited by the cue.

The role of beta synchrony in biasing response competition appears not only related to a biasing role of alpha activity in the selection of visual information (Worden et al. 2000; Kelly et al. 2006; Thut et al. 2006; Rihs et al. 2007), but also to the concept of “focal desynchronization/surround synchronization” (Pfurtscheller and Lopes da Silva 1999). The authors’ examples supporting this concept comprised antagonistic behavior of the rolandic mu rhythm and occipital alpha as well as antagonistic modulation of mu activity over hand and foot motor cortex. However, Pfurtscheller and Lopes da Silva (1999) also observed concurrent desynchronization and synchronization of beta activity over left and right motor cortex during motor imagery. Our data extend this observation and provide evidence that the antagonistic modulation can reflect a mechanism supporting the selection and suppression of competing responses. Related evidence for antagonistic modulation of competing response options comes from movement-related EEG potentials (Vidal et al. 2003; Praamstra and Seiss 2005), from transcranial magnetic stimulation (Leocani et al. 2000; van den Hurk et al. 2007), and from single-unit recordings in primates (Cisek and Kalaska 2005).
Within the context of research on the functional and anatomical loops connecting basal ganglia and cortex, it has been proposed that tuning of neural activity to different frequency bands may reflect a means of marking and segregating ongoing processes in different cortical-subcortical circuits (Fogelson et al. 2006). The operation of similar selection mechanisms carried by different frequency bands is in broad agreement with this proposal. With respect to selection operations carried by the sensorimotor beta rhythm, do the present results support the notion that differential modulation of beta-range activity implements a mechanism for the online selection between competing responses? If such a mechanism operates through antagonistic modulation of cortical beta power, then our data do not support the notion, because we found downregulation but not simultaneous upregulation of beta power. However, if the mechanism has a more complex mode of action, involving different components of beta-range oscillations, then our data do provide support for the investigated role, given the upregulation of corticospinal synchrony. The latter version probably represents a more plausible mechanism, recognizing that there are multiple components to the sensorimotor beta rhythm (cf. Jensen et al. 2005). Of relevance here, at the level of the striatum, task-related beta desynchronization occurs very focally amidst widespread beta oscillatory activity, giving rise to the proposal that beta oscillatory synchrony operates as a spatiotemporal filter to sharpen action-selection by corticobasal ganglia networks (Courtemanche et al. 2003). The regulation of corticospinal synchrony during the selection between competing response options would fit the concept of such an action-selection network. This would mean that beta-range corticospinal synchronzation is not exclusively a low-level motor control mechanism (Kilner et al. 2002).