Modulation of oscillatory neuronal synchrony in the beta band by motor set¹

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Oscillatory neuronal synchrony is thought to play an essential role in the neuronal processing of information. Modulation of these ongoing oscillations is a possible mechanism by which processing can selectively be biased. Evidence is presented for a modulation of oscillatory neuronal synchrony by motor set, obtained with magnetoencephalography. Subjects performed a bilateral isometric contraction and were cued in some trials to respond at the event of the imperative go-cue with a left and in others with a right wrist extension. The analysis of the period in which subjects could expect the go-cue to occur (stimulation period) revealed that beta power (15-30 Hz) was lower over the motor cortex when it was contralateral to the effect was due to a decrease in beta power in the stimulation period compared to baseline that was bigger for the motor cortex driving the cued side. Force output was equal in the two conditions and stratification of the EMG signals did not change the results. The location of the maximal decrease in beta power, and analysis within these channels also showed the same results. We conclude that motor set results in a selective modulation of beta power during a steady bilateral contraction.

Keywords: motor set, oscillatory synchrony, MEG, EMG.

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1 Introduction

The active brain

Traditionally, the brain was thought of as a passive stimulus-driven device, triggered by sensory inputs. This device supposedly had the objective to arrive at a context-invariant internal world model by reconstructing object properties in a hierarchical feedforward mode. Such an approach of human information processing tends to deal with perception and action in isolation (Hommel, Müsseler, Aschersleben, & Prinz, 2001). The alternative viewpoint is to see the brain as a much more active and adaptive device (Engel, Fries, & Singer, 2001). The latter view stresses the close linkage between perception and action. Instead of constructing context-invariant world-models, action (planning) guides perception and action is guided by perception. For example, the pattern of saccadic eye-movements during inspection of a painting varies dramatically with a priori instructions (Yarbus, 1967). Findings from singlecell recordings have often seemed to be in line with the traditional view of the brain consisting of hierarchical levels of specialized detectors extracting information from bottom-up input. Recently, however, there has been a great deal of evidence of top-down influence even in cortical areas at the bottom of the hierarchy (Treue, 2001; Lee, Yang, Romero, & Mumford, 2002)

Oscillatory neuronal synchrony

Sensory stimulation evokes responses in brain areas that are time- and phase-locked to the onset of the stimulus. These evoked components therefore survive averaging over trials while the procedure reduces noise that is assumed to be independent between trials and also components that are not phase-locked to the stimulus. A wellknown example of such an evoked component is the N400, elicited at a latency of about 400 ms by a semantic violation in a sentence (Kutas & Hillyard, 1980). Another thing we know is that brain shows spontaneous periodic oscillations in activity. By means of spectral analysis we can break down a signal into its different frequency components, like a prism breaks down light into components with different wavelengths. The idea originally proposed by Fourier was that we can decompose any mathematical function into a weighted sum of sinusoids that have a certain frequency and phase. Hence, analysing a signal in terms of its spectral components is called Fourier analysis. It allows for a compact representation of a periodic signal as a function of frequency instead of time. Traditionally, the frequency axis has been

subdivided into different bands for classification of neuronal oscillations, namely δ (0.5-4 Hz), θ (4-7 Hz), α (8-12 Hz), β (15-30 Hz) and γ (30-90 Hz). spontaneously An example of occurring oscillations are the different brain rhythms that occur during sleep and wakefulness; whereas the spectrum during slow wave sleep is dominated by high amplitude and low frequency oscillatory components, activated states like wakefulness and REM sleep are characterized by low amplitude and high frequency oscillations (Llinás, Urbano, Leznik, Ramírez, & Marle, 2005). These neural spontaneously oscillations occur but are modulated by (sensory) processing. An example of this is the increase in power at the alpha frequency over visual cortex when the eyes are closed. Recently the term induced component has been coined for components that are time-locked to sensory events but not necessarily phase-locked (see for example Makeig, 1993). In other words the latency of the effects is jittered in the different trials. These components can be detected by first performing spectral analysis on single trials before averaging (Tallon-Baudry & Bertrand, 1999). Evoked components can be considered to be signatures of the passive brain: input at time t leads to a certain component at time t + some fixed latency at a given location. The timing of an induced component on the other hand depends both on the time of input and the ongoing activity in the brain. Modulation of ongoing rhythms in the cortex can make brain regions more or less responsive to input. Besides looking at oscillations at a certain location we can also look at relationships between oscillations at different locations. Coherence and the closely related phaselocking are measures of interdependence in the frequency domain, similar to correlation as a measure of relatedness of signals in time. They quantify the consistency of the phase difference between two signals. Functional coupling of two sources leads to a consistent phase difference between their signals and a high coherence value.

What is oscillatory neuronal synchrony good for?

In the primate visual system more than 30 distinct cortical areas have been identified by physiological and anatomical studies (Felleman & Essen, 1991), reflecting functional specialization. The binding problem is: how do we keep processing together that belongs together and apart from processing that belongs to something else if it is distributed across the brain? One proposal is to use a temporal code that is independent of a rate code (the firing rate of neurons), to code for relations, allowing for selective and dynamic tagging of neurons that currently participate in the same cognitive process by specific yet flexible, contextdependent binding of distributed activation (Malsburg & Schneider, 1986; Engel et al., 2001). Briefly, the advantages of a temporal binding mechanism can be summarized as follows (Engel, Fries, König, Brecht, & Singer, 1999). First, it keeps the general advantages of distributed coding schemes like robustness against loss of network elements (graceful degradation) and representations which contain explicit information about object features instead of just signalling the presence of the object. Second, temporal binding can occur using the very first spikes of a response, suggesting advantages for the speed of processing (Fries, Neuenschwander, Engel, Goebel, & Singer, 2001). Third, temporal binding offers a solution to superposition problems, because it dissociates the relational (temporal) code from the feature code (firing rate). Fourth, temporal binding provides an efficient mechanism for selection of assemblies for further processing because precisely synchronized spikes constitute highly salient events and can be detected from random synchronizations. This can activate coincidence-sensitive neurons in other brain areas (König, Engel, & Singer, 1996). Although the idea of binding by synchrony is still controversial (see for a critical evaluation Shadlen & Movshon, 1999) experimental results point to special role for oscillations in the gamma band in visual binding (Gray, König, Engel, & Singer, 1989; Eckhorn, Frien, Bauer, Woelbern, & Kehr, 1993; Rodriguez, George, Lachaux, Martinerie, & Varela, 1999; Tallon-Baudry & Bertrand, 1999). However, the binding problem is not specific for the visual system and presumably also exists in other brain areas. Recently, an extension of the functional role of neuronal oscillations in visual binding to the coordination of neural processing in general has been suggested (Schnitzler & Gross, 2005): findings suggest that network oscillations bias input selection, temporally link neurons into assemblies, and facilitate synaptic plasticity (Buzsáki & Draguhn, 2004). In line with this general role findings are suggestive of a possible functional significance of oscillatory synchrony in motor functioning (Fetz, Chen, Murthy, & Matsumura, 2000; Salenius & Hari, 2003). Especially oscillations in the beta band have been found to be ubiquitous in the motor system. One suggestion is that the role of beta band activity is similar to that of alpha activity in visual cortex that supposedly reflects cortical idling (Pfurtscheller, Stancák, & Neuper, 1996). Another suggestion is that beta activity may be related to maintenance of posture (Gilbertson et al., 2005).

Attention and motor set

Attention is a cognitive function that is directly linked to neuronal information processing. As Hebb (1949) formulated it: "in the simplest terms, attention refers to a selectivity of response". The study of attention is often the study of perceptual selectivity; for example two visual stimuli are present in the visual field and the subject is instructed to attend to only one. The effect of attention is then the difference between the response to the target and the response to the distracter. Again oscillations in the gamma band have been related to visual attention (Fell, Fernández, Klaver, Elger, & Fries, 2003). Fries (2001) recorded neurons in V4 while macaque monkeys attended behaviourally relevant stimuli and ignored distracters and found that neurons activated by the attended stimulus showed increased synchronization in the gamma band (35-90 Hz) but decreased synchronization at lower frequencies (<17 Hz) compared with neurons activated by distracters. The idea is that localized changes in synchronization reflect amplification of behaviourally relevant stimuli because gamma band synchrony may be more effective in activating postsynaptic neurons. These neurons have an enhanced sensitivity to synchronous synaptic inputs that lead to rapid rates of depolarization while they actively compensate for slow changes in mean input rate (Azouz & Gray, 2003). Attention is selectivity in what is responded to or sensory selectivity while the term set is used for selectivity of motor response (Hebb, 1972). In the current study we considered selectivity in the motor system and therefore use the term motor set. By using the term set instead of attention we also mean to avoid the confusion that the latter can cause. Sometimes attention and awareness are seen as related concepts (Crick & Koch, 1990) and selective attention is thought to correspond to selective awareness (for arguments to separate the two see Lamme, 2003). We want to avoid this connotation of awareness that attention has and motor set much less by using the latter term. Oscillatory synchrony is proposed to have a functional role in neuronal information processing. Modulation of this ongoing activity can then selectively bias neuronal information processing in such a way that certain input to a brain region is processed more efficiently than other input. Therefore we hypothesize that motor set modulates ongoing oscillatory activity in the cortex.

Aim of project

We addressed the question whether oscillatory neuronal synchrony is affected by motor set. To this end, we aimed at activating motor cortices in a task that required subjects to use the visual information in order to control the motor output. Subjects were trained to hold both wrists extended during the presentation of a visual stimulus. The visual stimulus displayed a change at an unpredictable moment in time after its onset. Subjects responded to the stimulus change with a further extension of one of the wrists. We wanted to assess the effect of our experimental manipulation during constant and equivalent motor output on both sides. To ensure this, force calibration was necessary: the subject had to move both forces within a narrow window and hold the bilateral contraction steady. Power in the beta band is know to show a rebound after movement (Pfurtscheller et al., 1996), therefore we looked at the periods some time after force was calibrated and steady in order for the beta power to have returned to baseline levels. The crucial experimental manipulation in this experiment was that the subject was cued to respond in some trials with the left and on other trials with the right wrist. In other words, the subject was set to respond on the cued side. Apart from the cuing, the trials were physically identical. We expected that the manipulation of response side would have an effect on oscillatory neuronal synchrony in motor cortex. In particular, activity should be qualitatively different in motor cortex when it is contralateral to the response side compared to when it is contralateral to the side where abstinence of response is required. This effect should be maximal when the subject's set to respond is the biggest, namely in the period in which the go-cue can occur

MEG and EMG

One functional unit of the brain is the neuron and its input stations are the dendrites that receive a combination of excitatory post-synaptic potentials (EPSP) and inhibitory post-synaptic potentials (IPSP) over which integration takes place. Basically the effect of synaptic activity is to determine the frequency with which action potentials are generated. The local field potential (LFP) is an extra-cellular measure of the fluctuations in the membrane potentials of a group of neurons and mainly reflects the input to the population. Oscillations of the LFP therefore reflect regularities in the input of a population (Schnitzler & Gross, 2005). Because were interested in oscillations of the LFP we used MEG to record the electrophysiological signal with the required high temporal resolution. The potential recorded at the scalp consists of spatially averaged LFPs and therefore represents the summated

membrane potential fluctuations as well as action potentials (Nunez, 1995). It has been argued that the dominating components in the signal are the post-synaptic membrane potentials of mainly large pyramidal neurons (Baillet, Mosher, & Leahy, 2001). MEG picks up the magnetic fields corresponding and perpendicular to these currents. Since the magnetic field gets through intervening tissues basically unchanged, in contrast to the current, the spatial blurring of the source activity at the sensor level is less in MEG than it is in EEG (Lütkenhöner, 2003). In this study our focus is on the oscillatory neural activity in the MEG sensors overlying motor cortex and visual cortex. The MEG signal is strongly enhanced by temporal synchronization of the underlying activity; therefore power changes in a channel at a certain frequency indicate local changes in synchrony. Importantly, we first calculate the power for every single trial before averaging so that we pick up induced components that are time- but not necessarily phase-locked to events. We also recorded the electromyogram (EMG). Alpha-motor neurons in the spinal cord innervate groups of skeletal muscle fibers at neuromuscular junctions. The neuromuscular junction acts as a single relay synapse: the activity of the motor neuron has a one-to-one correspondence to the activity of the muscle. The motor neuron on the other hand requires concurrent activation of numerous excitatory inputs and is driven predominantly by the contralateral primary motor cortex (Randall, Burggren, & French, 1997). Surface electromyography (sEMG) allows for noninvasive measurement of the electric potential field evoked by active muscle fibers (Zwarts & Stegeman, 2003) and reflects the activity of the alpha-motor neuron that innervates the fibers.

activity of subthreshold soma and dendritic

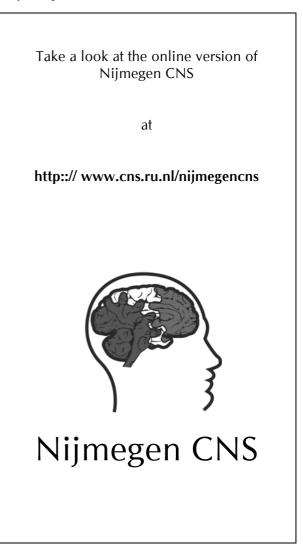
2 Methods

2.1 Participants and paradigm

10 healthy subjects (4 female, mean age 24 years, range: 21-28) participated in the experiment. All subjects gave written informed consent according to the Declaration of Helsinki. We were interested in the activity in the brain (the MEG signal), the activity of the muscles (the EMG signal) and the relationship between the two. For this we designed a cued simple reaction time task. In this task the subjects performed а bilateral isometric contraction of the extensor carpi radialis longus, the muscle that extends the wrist when activated. In an isometric contraction the muscle is activated but held at a constant length so that there is a constant correspondence between force output and muscle activity. It was important in our paradigm that measurements were obtained during a constant force output. To this end we required the force signal to be within a prespecified range during a trial. A schematic outline of a typical trial is shown in figure 1. In the top of the figure the left and right force traces are shown. The two black lines indicate the upper and the lower border of the desired force output. In the bottom part of the figure the time axis is shown and the corresponding visual stimulation. At the beginning of every trial a cue was presented that was either an arrow to the left or to the right, instructing the subject to respond to the appearance of the go-cue with the left or right hand. After this the force calibration started in which subjects fixated the central cross and extended both their wrists to elevate their hand against the levers of two force meters to bring the measured forces into a prespecified window, the exact settings of which were adjusted to obtain about 15 % motor unit recruitment. When the force got into the window the traffic light turned from red to green. In the figure these two traffic lights can be seen left and right from the fixation point, informing the

subject about whether respectively the left force and the right force were in the window (green light) or not (red light). If both forces were in the window for 1000 ms the traffic lights disappeared and the subjects fixated a fixation point while holding the bilateral contraction steady. Then after another 1000 ms the visual stimulation started. The visual stimulus was a concentric sinusoidal grating, contracting towards the fixation point (diameter: 5, spatial frequency: 2 cyc/deg, contrast: 100 %, velocity: 0.8 deg/s) and the speed change (velocity step to 1.6 deg/s) could occur at an unpredictable moment between 150 and 3000 ms after stimulus onset. The speed change of the visual stimulation was the go-cue. The subject had to respond in time by exerting more force to the lever by a more extreme wrist extension at the cued side. Thereby the force moved out of the window while the contraction on the side that was not cued was kept constant. If the subject's force exited the window before the go-cue appeared the trial was stopped and error feedback was given. In both conditions, about 10 % of the trials were catch trials and did not contain a speed change, in which case the correct response consisted of maintaining the wrist extension until stimulus offset. Subjects were given feedback after each trial. The duration of a trial was variable: the cue and the fixation point were on for 1000 ms, force calibration lasted maximally 5000 ms of which both contractions needed to be OK for the last 1000 ms, and finally the period until the speed

change was variable between 150 ms and 3000 ms. The trial effectively started when force calibration was successful. The bilateral experiment consisted in total of 300 trials divided over 6 blocks. Summarized, subjects performed a simple reaction time task in which they were cued to respond to a go-cue. Subjects maintained throughout the trial a constant bilateral isometric contraction after the force calibration. In order to be able to localize the motor cortices with the use of an independent data set (see also section 2.3.2) we also let the subjects perform a simple unilateral contraction: in the first block of 20 trials a left wrist extension (LC) was required to bring the force within the force window for the length of 8000 ms, then in the second block of 20 trials the same was asked of the subject for the right side (RC). Every session started with a short training of about half an hour on the bilateral task the subject needed to After this, recording perform. of electrophysiological signals started. First the subjects performed the unilateral contraction task. Finally the subjects performed the bilateral task they had practiced.



Go trial for condition left desired force level = force left_ desired force level = force right force calibration fixation point speedchange movie cue stimulus 1000 ms 0~4000 ms 1000 ms 1000 ms 150~3000 ms 150+450 ms Baseline

Figure 1: Experimental paradigm.

2.2 Stimulus presentation and data collection

Stimuli were presented with an LCD-projector, with an update frequency of 60 Hz. Control measurements with a sensitive photo-diode showed no 60 Hz component in the luminance time course of the stimuli. Force applied to the levers was measured by strain gauges. For the measurement and real-time control of generated force output we used an A/D conversion system. Apart from being recorded in parallel with the electrophysiological data, custom-made window discriminator software that received the two force signals as input via the A/D convertor was used to detect whether the force was within the prespecified window. For our data collection

we used the CTF MEG system at the Donders Centre, including its EEG and EMG recording capabilities. MEG was acquired with a 151-sensor axial gradiometer system. Bipolar surface EMG was recorded from the left and right m. extensor carpi radialis longus using 2 Ag/AgCl electrodes, which were placed over the muscle with a 2-cm interelectrode distance, with the proximal electrode placed 2 cm distal to the external epicondyle of the humerus. The EOG was recorded from a bipolar electrode pair placed above and lateral to the outer canthus of the left eye. The impedance of the EMG and EOG electrodes was below 20 kOhms. The data were low-pass filtered at 300 Hz and digitized at 1200 Hz. Prior to and after the MEG recording, and between blocks, the subject's head position relative to the gradiometer array was determined using coils positioned at the subject's nasion, and at the bilateral external auditory meatus.

2.3 Data Analysis

2.3.1 EMG- and MEG-signal preprocessing

All analyses were done with Matlab and using FieldTrip, an open source software package for EEG and MEG data analysis, developed at the FC Donders Centre¹. In a correct go trial the subject kept both force left and right within the window during the period until the go-cue and then responded in time with the cued side while keeping the force on the other side within the window. In a correct no-go trial the subject just had to keep both force left and right within the window during the entire duration of the trial. On average, the experimental sessions with 300 trials vielded 83% correctly performed trials. Data segments that were contaminated by eve movements, muscle activity or jump artifacts in the SQUIDs were discarded. We removed the powerline artifact using a DFT filter and the linear trend in the data. EMG-amplitude was estimated by high-pass filtering the raw EMG signal at 10 Hz and then taking the absolute value of its Hilbert-transform. This procedure enhances firing rate information in the signal and is equivalent to full rectification of the EMG-signal (Myers et al., 2003). The measured axial gradients of the magnetic field were transformed to planar gradients using a nearest neighbour interpolation (Bastiaansen & Knösche, 2000). This facilitates the interpretation of the MEG topography across subjects.

¹ Fieldtrip toolbox for EEG/MEG-analysis. FC Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands. http://www.ru.nl/fcdonders/fieldtrip

Stratification procedure

One potential problem might emerge if subjects contract to different degrees on the cued and noncued sides. For this reason we monitored whether the force exerted on the lever was within the force window. However, the activity of the muscles could be different even with equal force output. Different patterns of co-contraction of agonist and antagonist muscles or differences in the position on the lever where the force is exerted could in principle be systematically related to conditions. We therefore wanted to check whether differences between conditions were observed while the distributions of the mean amplitude of the EMG, a measure of the activity of the muscle, were not significantly different across conditions. We first calculated the mean amplitude per trial by bandpass filtering the raw EMG signal between 10 and 250 Hz and subsequently applying the Hilbert transform, which gave us an estimate of the instantaneous amplitude. Stratification ensures that the distribution of the average amplitude in trials of condition left is equal to the distribution of the average amplitude in trials of condition right. We tested the significance of the difference between two distributions by evaluating it under a reference distribution we obtained by shuffling the trials between conditions. To make a selection of trials with similar distributions of the average amplitude both for the left and right EMG in the two performed conditions we the following stratification procedure (see also for example Roelfsema, Lamme, & Spekreijse, 1998). First we chose a number of bins. The choice of the number of bins is arbitrary and has an effect on the number of trials thrown away and the resolution at which we make two distributions equal. In the extreme case of just one bin, only the number of trials will be equated. Using different numbers of bins suggested that choosing 5 bins gave the best trade-off between on the one hand making the distributions similar and on the other hand not throwing away too many trials. We created a common bin space for the two distributions together of which the centres were chosen to maximally account for the spread of the data. Separately for the left and right EMG we had J bins where every bin j contained n trials for condition left and m trials for condition right. We then randomly threw away trials until $n_i = m_i$ so that the number of trials left over in a bin was the minimum of n_i and m_i. Finally we selected the trials that were both left after stratification of the left EMG and the right EMG, that is the intersection.

2.3.2 Analysis of average power and coherence

We used two time periods from the experimental task (see figure 1 on page 7) for the analysis of the average power and coherence spectra. The baseline (B) period is the interval from 1000 ms before the onset of visual stimulation until its onset. In this period the subject performs a steady bilateral isometric contraction and knows that the go-cue cannot occur in this period. The stimulation (S) period is from 300 ms after the onset of the visual stimulus until the speed change. In this period the subject also performs a steady bilateral isometric contraction but knows that the go-cue can occur in this period and is ready to respond. In condition left (L) the subject is cued to respond to the onset of the go-cue with the left wrist and in condition right with the right wrist (R). We calculated the average spectra in both conditions of the baseline periods (LB and RB) and of the stimulation periods (LS and RS). The critical and central comparison was between LS and RS, since we expected the effect of our manipulation of motor set to be mainly revealed in this period. The comparison between LB and RB was made to determine this effect in the baseline period. We also inspected the differences between the stimulation and the baseline period (LS vs LB and RS vs RB) because we expected the subject to be more set to respond in the period in which the go-cue could occur (P(go-cue appears) = 0 in the baseline period and P(go-cue appears) > 0 in the stimulation period). These differences between the stimulation and the baseline period were in turn compared between conditions (LS-LB vs RS-RB). Because the resulting data segments had a variable duration, they were first tapered, then zero-padded to a length of 4 s and then Fourier transformed. The Fourier transform $\tilde{x}(f)$ of a discrete time series $\{x_t \mid t = n\Delta t, n = 1, 2, \dots, N\}$ is given by:

$$\widetilde{x}(f) = \sum_{n=1}^{N} x_{t} e^{-2\pi i f n \Delta}$$

If *T* is the length of the time window, the frequency resolution is given by the Raleigh frequency $f_r = 1/T$. The digitization frequency is $f_d = 1/\Delta t = 1200$. According to Nyquist theorem only frequency components that are not bigger than the Nyquist frequency, $f_n = 1/2$ f_d , can be reconstructed if they are present in the signal. Data was low-pass filtered by an analog filter with a cut-off frequency of 300 Hz. For the tapering of the data segments, we used the multi-taper method. We used a spectral smoothing of ± 2 for the cluster level test statistic, focusing on the lower frequency bands, and we used ± 5 for the group

level statistics in the selected sensor set (see for details on the statistical methods section 2.3.3), focusing on a wider range range of the frequency axis. The direct multitaper spectral estimate of time series x_{i} , is defined as the average over individual tapered spectral estimates,

$$S_{X}(f) = \frac{1}{K} \sum_{k=1}^{K} \left| \tilde{x}_{k}(f) \right|^{2}$$

with:

$$\widetilde{x}_k(f) = \sum_{n=1}^N w_t(k) x_t e^{-2\pi i f n \Delta t}$$

where $w_i(k)$, k = 1, 2, ..., K are K orthogonal taper functions (see Mitra & Pesaran, 1999, and references therein). The number of tapers for a data segment is determined by the frequency smoothing S and the length of the segment: K = 2(ST)-1. So for a data segment of 1 second 9 tapers are used with a frequency smoothing of ± 5 Hz. The spectra we obtain are complex valued, containing in polar notation an amplitude and phase at every frequency:

$$S_{X}(f) = A(f)e^{i\phi(f)}$$

We estimate the expected value of the spectrum by averaging over multiple realizations, i.e. number of trials in a certain condition (Bruns, 2004). From the spectra we can compute the power and coherence: The power is defined as the squared modulus of the spectrum and is also called the auto-spectrum (Challis & Kitney, 1991). The (squared) coherence between signals X and Y is the squared cross-spectrum divided by the autospectra of the signals:

$$C_{XY}(f) = \frac{|S_{XY}(f)|^2}{S_{XX}S_{XY}}$$

The cross-spectrum is:

$$S_{XY} = S_X \cdot S_Y^* = A_X(f) A_Y(f) e^{i(\phi_X(f) - \phi_Y(f))}$$

From this can be seen that coherence represents the consistency of the phase difference and that it is normalized between 0 and 1. Coherence estimates have a positive bias that decreases with an increase in the amount of data. To correct for this, a non-linear transformation can be applied to the coherence spectra (Jarvis & Mitra, 2001). In the following we will refer to the corrected coherence estimate as the z-transformed coherence (see also Schoffelen, Oostenveld, & Fries, 2005). We also used the simple unilateral contraction task for analysis. The trials were first cut into segments of 1000 ms after which the ztransformed coherence was calculated separately for the unilateral contraction left (LC) and right (RC) between the MEG sensors and the left and right EMG. After inspection of the coherence spectra a frequency band of 10 Hz was selected

around the peak frequency in every subject. Coherence was averaged in this band. Subsequently we took the difference between LC and RC, calculated the z-score over channels (so that the average was not dominated by subjects with the largest z-transformed coherence) and finally averaged over subjects. We then selected the 5 channels that were maximally coherent with the left EMG and the 5 channels that were maximally coherent with the right EMG. See figure 6 on page 15 for a sketch of the procedure.

2.3.3 Statistics

A prominent feature of cognitive processes is the large intersubject variability and a statistical analysis on the group level is therefore necessary to reveal the most prominent responses across the group (Hillebrand, Singh, Holliday, Furlong, & Barnes, 2005). We used two approaches to test the differences between conditions at the group level. The first approach was using a cluster level test statistic. The second approach was evaluating effects only in a prespecified region of interest. The rationale of using two different approaches is the following. First of all, if we find the same results with two different approaches this will cross-validate the two methods and provide further support to the results. Another reason is that two methods have different advantages. The cluster-level test statistic makes no prior assumptions about where the effects are located and therefore shows the most prominent effects in the entire sensor space. The region of interest approach uses the sensible criterion of the maximal coherence with the EMG in an independent data set for localizing motor cortices, since the motor cortex is known to drive the contralateral muscle. Therefore it supports the idea that we are looking at motor cortex if we limit our analysis to the two regions that are selected on the basis of this criterion. Furthermore, we would expect increased power of detecting effects in motor cortex with this approach. Moreover, the channel selection can be used as a reference region for computing cortico-muscular or corticocortical coherence. The two approaches will be described in more detail below.

Cluster level randomisation test

The multiple comparisons problem is the name for the fact that the false alarm rate (the probability with which we reject our null hypothesis while it is true) increases with the number of comparisons. This problem is often encountered in cognitive neuroimaging because of the high dimensionality of the data. Nonparametric statistical inference is well suited

for dealing with this kind of data (Maris & Oostenveld, 2005) and the multiple comparisons problem can be solved by reducing multiple test statistics to just one aggregate test statistic. This approach also allows us to use a test statistic that incorporates a priori constraints that are biophysically plausible. The cluster level randomisation test uses a test statistic at the cluster level since effects in planar MEG sensors are clustered in space and frequency. For every subject we compute an average spectrum in condition A and B giving us a paired sample. Our null hypothesis of no effect is that conditions are exchangeable within subjects. The cluster level randomisation test works in the following manner. First a test statistic is calculated for every frequency channel combination, in this case by using a paired samples t-test. Connected clusters are then constructed of samples that have the same sign of the test statistic. The test statistics of the clusters are obtained by taking the sum of the individual samples' test statistics in the cluster. These cluster level test statistics are evaluated under the randomisation distribution of the maximum of the cluster-level statistics: for 1000 randomisations conditions are randomly shuffled within subjects and the maximum cluster level statistic is put in the reference distribution. Evaluating significance under this reference distribution will control the false alarm rate. See Maris (2004) for an extensive discussion of the rationale behind the cluster level randomisation test. In the following, whenever we use the term cluster analysis, we mean the approach that uses a cluster level randomisation test.

Group level statistics in selected sensor set

In our second approach we reduce the number of comparisons by first averaging over a selection of 5 sensors based on an independent data set. The independent samples t-test is calculated as a measure of the difference between the two conditions at the single subject level.

$$t = \frac{(\overline{x}_1 - \overline{x}_2)}{\sqrt{\frac{s_1^2(n_1 - 1) + s_2^2(n_2 - 1)}{(n_1 + n_2 - 2)} \left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

We now have a matrix T_{diff} with dimensions number of subjects x number of frequency bins containing in every cell a t-statistic of the difference between conditions A and B. Our teststatistic simply is the average over N subjects for every frequency. To test the significance of the effect at the group level we again use a nonparametric test. Under the null hypothesis of no effect conditions are exchangeable within subjects. The t-statistic of the difference between condition A and B basically is a paired sample. We obtain a reference distribution by calculating the value of the test-statistic for every possible relabeling of conditions within subjects by multiplying the tvalue of one subject with a multiplication factor of either m = 1 or m = -1. The number of relabelings R is 2^N . The multiplication factor matrix has dimensions number of relabelings x number of subjects. Multiplying the multiplication factor matrix with T_{diff} results in a distribution T_{rlb} of the test-statistic for every frequency band with dimensions number of relabelings x number of frequency bins. To solve the multiple comparisons problem across frequencies and control for the false alarm rate we created a reference distribution by putting the maximum t-value over all frequency bands of a given relabeling in the reference distribution. Concretely, we take the maximum of T_{tb} over the second dimension frequency and normalize for the number of subjects. The p-value is given by the proportion of relabelings that is more extreme than the test-statistic and the critical values are the $1/2\alpha \cdot R + 1$ smallest and largest members of the reference distribution in a twosided test (Nichols & Holmes, 2002).

3 Results

Behavioural results

The average performance of the subjects in the task was as follows. The mean reaction time was 376 ms and subjects performed on average 83 % correct. Neither the average mean reaction time nor the percentage correct were significantly different in condition left and right in a paired sample t-test (respectively p=0.449 and p=0.447, randomisation tests).

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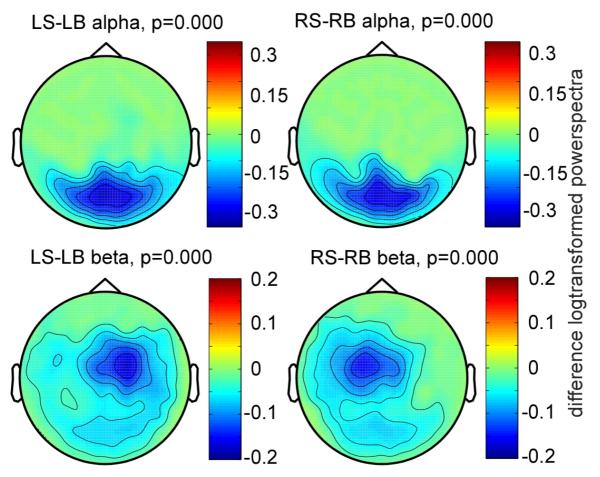


Figure 2: Cluster analysis Results. Alpha band is 8-12 Hz, Beta band is 15-30 Hz. Plotted and on the colorbar are the differences in the logtransformed powerspectra of the two conditions that were significant.

MEG power in stimulation and baseline period

The comparisons we make are between the estimates of the average spectra in both conditions of the baseline periods (LB and RB) and of the stimulation periods (LS and RS) that we calculated for every subject. We test significance at the group level of differences between the averages over subjects. We first discuss the results of the cluster analysis we applied to test significances. Second, we will show the results of the region of interest approach.

3.1 Cluster level randomisation test

Power is known to drop off roughly according to 1/f; the power of the spectrum S(f) obtained with MEG is inversely proportional to the frequency. 1/f power drop-off is a phenomenon observed in a wide variety of signals, for example the velocity of ocean waves and the loudness of natural sounds (Yu, Romero, & Lee, 2005). However, we are not

interested in the absolute magnitude of signals at a certain frequency but rather in the relative differences between conditions. We therefore use the difference of the logtransformed powerspectra in condition A and B, which is equivalent to the ratio of the powerspectra, to inspect relative differences.

Cluster analysis: alpha and gamma power

Comparing the stimulation period to the baseline period within conditions we observe the following results. First the alpha band power (8-12 Hz) decreases dramatically (see top of figure 2) while the gamma band (40-80 Hz) power increases in the occipital sensors in the stimulation period (see figure 3). This effect appears both in condition left and right.

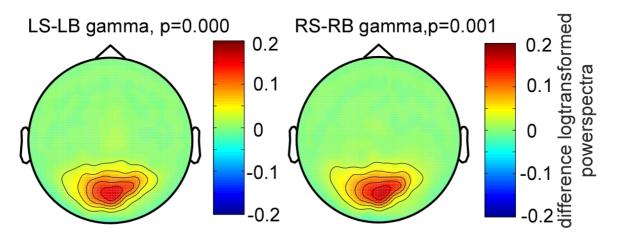


Figure 3: Cluster analysis Results. Plotted and on the colorbar are the differences in the logtransformed powerspectra of the two conditions that were significant. The comparison between the logtransformed powerspectra in the stimulation and baseline period reveals an increase on gamma power (40-80 Hz) in both conditions left and right.

Cluster analysis: stimulation vs baseline: beta power

Second, the power in the beta band (15-30 Hz) decreases significantly in the stimulation period

relative to the baseline period. This decrease is lateralized in that it is bigger over the motor cortex contralateral to the side that needs to respond compared to the motor cortex that needs to abstain from responding (see bottom of figure 2).

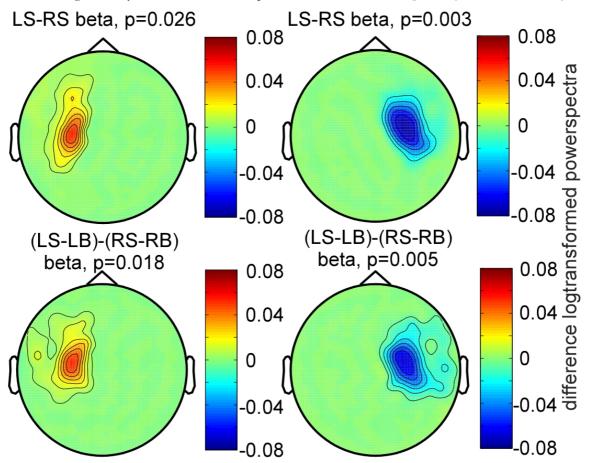


Figure 4: Cluster analysis results. Plotted and on the colorbar are the differences in the logtransformed powerspectra of the two conditions that were significant. In the upper panel the comparison is between the logtransformed powerspectra in condition left and right in the stimulation period yielding a significant positive and a significant negative cluster in the beta band (15-30 Hz). In the lower panel the comparison is between condition left and right after correction by the baseline period.

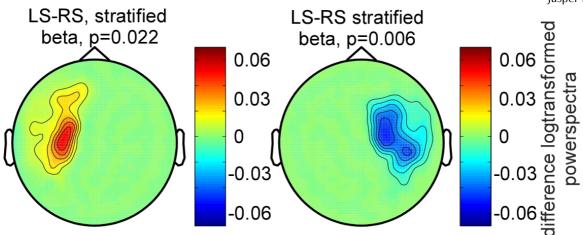


Figure 5: Cluster analysis Results. The same comparison and general format as in figure 4 after stratification.

Cluster analysis: condition left vs condition right: beta power

The results of the comparison between condition left and right (L-R), where the only difference is that the subject is set to respond with the left respectively right hand, are shown in figure 4. The power in the beta band (15-30 Hz) in condition left is bigger over left motor cortex and lower over right motor cortex compared to condition right (top of figure 4). In other words, beta activity over left motor cortex is lower in condition right and beta activity over right motor cortex is lower in condition left. In the baseline period no significant differences are revealed by cluster analysis. We have also made the comparison between the baseline controlled stimulation periods in both conditions. To this end we first took the difference between the stimulation period and the baseline period within a condition and subsequently compared these between the conditions. Again we see the left lateralized increase and a right lateralized decrease. That is, power in the beta band decreases more when the hemisphere is contralateral to the side that needs to respond than when it is contralateral to the side that is not cued (bottom of figure 2 and bottom of figure 4). Besides the significant differences over motor cortex no differences were found. This is clear support for the notion that only activity over motor cortices was lateralized.

Stratification procedure

In order to exclude the alternative explanation that observed differences were due to lowerlevel differences between condition left and right we performed a stratification procedure on the EMG. The stratification was dependent on the amount of spectral smoothing since we first had to select the trials that were long enough for a given smoothing. The stratification was then performed on this pre-selection. The stratification procedure resulted in a trial selection in which the distributions of the mean amplitude of the left and right EMG were not different across the two conditions (for all subjects p > 0.25, randomisation test). As shown in figure 5 the difference between condition left and right in the stimulation period is still present after stratification (for the result without stratification see top figure 4). This supports the idea that this effect does not result from differences between conditions at the level of the EMG.

3.2 Group level statistics in selected sensor set

Defining a region of interest using prior information

The result of the channel selection based on the unilateral contraction task is shown in figure 6. This procedure gives us an independent and sensitive indication of the location of the motor cortices.

The topography of the two selected groups is highly similar to the two clusters in which the maximal decrease in the beta band power was observed. The average z-transformed coherence in the unilateral task is shown in figure 7. During an extension of the left wrist coherence exists almost exclusively between the left sensor group and the right EMG and during an extension of the right wrist coherence is mainly observable between the right sensor group and the left EMG.

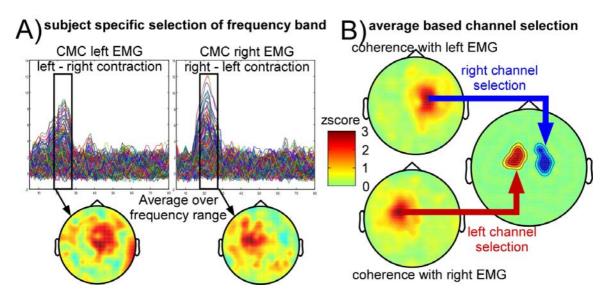


Figure 6: Coherence in a unilateral contraction. In A the CMC of all MEG channels with the EMG is shown. We first select a subject specific frequency band over which we average the CMC with the left and right EMG. The z-score is then taken, indicating which channels show the largests deviations in a subject, and subsequently averaged over subjects. Finally, the 5 channels with the maximum CMC with the left (channel sel right, since left EMG is maximally coherent with contralateral MEG sensor group) and right EMG (channel selection left) are selected (B).

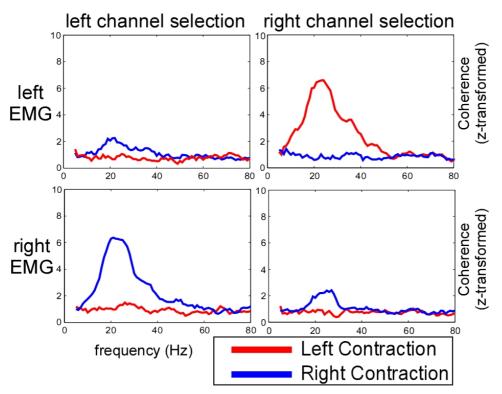


Figure 7: Coherence in channel selection during unilateral contraction task.

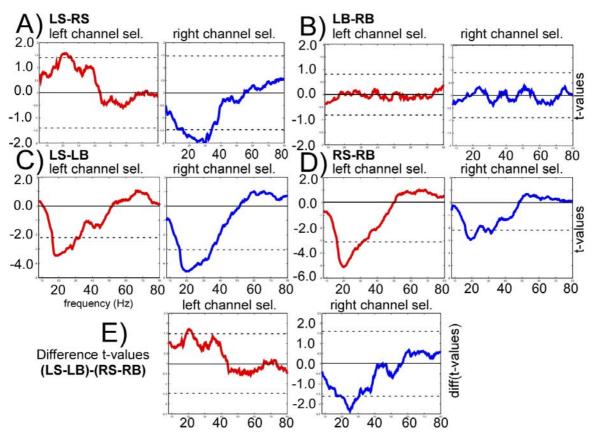


Figure 8: T-values of differences between power in experimental conditions. Dotted lines are the critical values with $\alpha = 0.05$, corrected for multiple comparisons.

Analysis in ROI

In the channel selection, that had been determined with the procedure described above, we were able to confirm the results of the cluster analysis. Depicted in figure 8 are the average t-values of the differences for all considered comparisons and the corresponding critical values of the reference distribution with $\alpha = 0.05$, corrected for multiple comparisons (see methods section). The left channel selection shows both in condition left and right a significant decrease relative to baseline (left plots 8C and 8D) but this decrease is bigger in condition right (left plot 8E). The right channel selection shows both in condition left and right a significant decrease relative to baseline (right plots 8C and 8D) but this decrease is bigger in condition left (right plot 8E). The direct comparison of the stimulation periods (8A) shows that the beta power is bigger in the left and lower in the right channel selection in condition left relative to condition right. Interesting is furthermore that the plots suggest that the effect at the higher frequencies (50-80 Hz) is inverted to the beta power effect in that it is bigger in the hemisphere that has to become active, although this is not significant. The direct comparison of the baseline periods (8B) in the two conditions shows no difference.

Cortico-muscular coherence

Cortico-muscular coherence was calculated between all pairs of the EMG channels and the MEG channels. Although the focus in this article is on the effects in power, we make some observations about the cortico-muscular coherence at a descriptive level. In figure 9 we compared condition left to condition right, both in the stimulation and the baseline period. Shown is the average z-transformed CMC in the left channel selection with the left EMG and with the right EMG, in the stimulation period and in the baseline period. The same is shown for the right channel selection. It appears that the average ztransformed

coherence is not different across condition left and right. Again, only the coherence spectra between the EMG and the MEG group contralateral to it show convincing peaks. In figure 10 we compared the stimulation period and the baseline period, both in condition left and condition right. Shown is the average ztransformed CMC in the left channel selection with the left EMG and with the right EMG, in condition left and in condition right. The same is shown for the right channel selection. Here it appears that the average z-transformed coherence in the beta band is generally lower in the stimulation than in the baseline period and this only holds for the coherence between the EMG and the contralateral

4 Discussion

Stimulation versus baseline period

In advance we hypothesized that motor set would modulate oscillatory neuronal synchrony in motor cortices. One of our expectations was that this effect should be maximal when the subject's set to respond was maximal. During the experimental task, the subject needed to monitor the visual stimulus for the imperative go-cue that occured at an unpredictable moment in time. However, the subjects did know that the go-cue had zero probability of appearing in the baseline period and nonzero probability of appearing during the stimulation period. Motor set will be bigger when the subject's expectancy to respond is bigger and therefore reflects knowledge about the likelihood of the occurrence of the go-cue. This can be the result of behavioural experience that allows a probalistic estimate of the time of the go-cue. Schoffelen (2005) showed that subjects can implicitly learn the so-called hazard rate, the probability that the go-cue occurs given that it hasn't vet occurred; the reaction time was inversely correlated with the hazard rate. Interestingly, power over motor cortex in the gamma band correlated positively while power in the beta band correlated negatively with the hazard rate. Riehle (1997) also found that go-cue expectancy affects spike synchronization in primary motor cortex in the absence of firing rate modulations. The comparison between the baseline and the

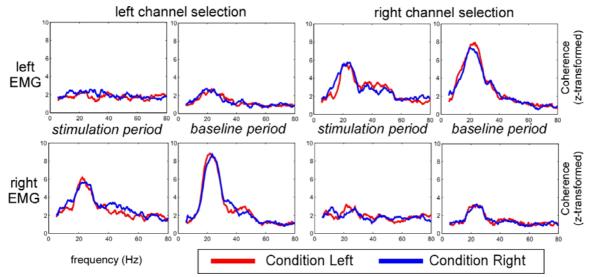


Figure 9: Coherence in channel selection during bilateral contraction task. Comparison between coherence in condition left and in condition right.

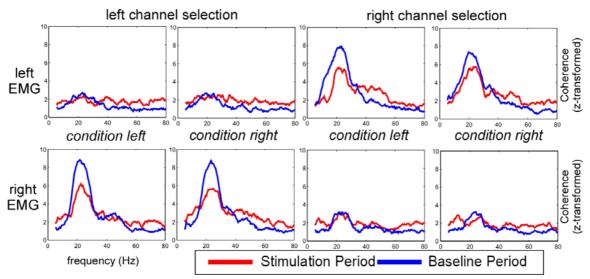


Figure 10: Coherence in channel selection during bilateral contraction task. Comparison between coherence in stimulation period and in baseline period.

stimulation period in condition left revealed a decrease in beta power both in the sensors overlying left and right motor cortex although the decrease was bigger in the sensors over right motor cortex. In condition right the decrease on both sides in beta power was also evident and bigger in the left sensor group. The comparison between the cortico-muscular coherence in the baseline and the stimulation period suggested that beta band coherence is generally more pronounced in the baseline period than in the stimulation period both in condition left and right. This had been previously shown by Schoffelen (2005) in a unilateral contraction.

Condition left versus condition right

We also predicted that activity in the motor cortex contralateral to the response side should show a qualitatively different pattern of activation compared to the motor cortex contralateral to the side where abstinence of response was required. At the start of every trial the subject was cued whether to respond with left or right wrist to the appearance of the go-cue. Thus, the subject is set to respond at one side to the go-cue: the contralateral motor cortex needs to drive the response while the ipsilateral motor cortex should not drive a response in the side that is not cued. The well known pre-cue utilization effect (see for example Gottsdanker & Shragg, 1985) describes the finding that reaction times become shorter when the subject is told in advance what the required response is to the imperative stimulus. This effect has been interpreted as the deletion of the response-selection stage; the subject already knows he has to respond in the case of a go-cue with the motor effector indicated by the cue. Described in the section above is the finding that the decrease in beta power in the stimulation period compared to the baseline period in condition left was bigger over right motor cortex while in condition right it was bigger over left motor cortex. The direct comparison between condition left and right reveals that in the stimulation period of condition left the beta band power is higher in the sensors overlying left motor cortex and lower in the sensors overlying right motor cortex compared to condition right. This effect of the cue that allows for response selection is present in the stimulation but not in the baseline period: so the difference in motor cortex when it is ipsilateral and when it is contralateral to the response side is only apparent in the stimulation period in which the go-cue can appear and the subject should be more set to respond than in the baseline period. The comparison between the

cortico-muscular coherence in condition left and right showed no obvious difference across conditions. Baker (2003) also found a relative constancy of corticomuscular coherence despite perturbations of the power of the EEG by pharmacological agents and interpreted this as suggestive for a functional role of corticomuscular coherence in itself.

Motor set or preparation

It is possible to distinguish between motor set and motor response preparation. Motor response preparation denotes the processes that precede a motor response. It is here defined as preparation while you know you can respond. Certain preparatory components have been identified that are time-locked to and precede the movement onset. For instance the readiness potential or Bereitschaftspotential is a slow negative potential preceding self-paced movements (Doyle, Yarrow, & Brown, 2005). The subject can start motor response preparation after he has perceived the imperative go-cue; we only consider the periods that precede the go-cue and don't look at these time- and phase-locked components. Motor set is located earlier in the causal chain that can eventually end with a movement. It is preparation while you know you may have to respond. In our task the subject is cued to respond either on the left or right side if and only if the go-cue appears. Thus, the subject can expect that he has to make a certain response but cannot set into motion the cascade of events that unavoidably lead to a movement before the go-cue appears. First, in some percentage of the trials the go-cue does not appear in which case the subject needs to abstain from responding (no-go trial) and second, the gocue appears at a certain time with a certain probability: although over multiple trials it may be more likely that it will appear at a certain time, in a given trial it can appear over a wide range in time with some small probability.

Motor set modulates beta band power over motor cortex

Our main conclusion is that motor set modulates oscillatory synchrony in the beta band in the motor cortices. Beta power was lower over motor cortex if it had to become active in case of the appearance of the go cue and less so if it had to keep a steady contraction. Crucially, these differences were observed during steady contraction and equivalent motor output and sensory input. Clearly, this modulation of activity by motor set pleads against the simple view of the motor cortex as an independent output module for motor commands. Although electrical

stimulation of motor cortex can evoke predictable behavioural responses and motor cortex is the cortical source that drives the muscles, this does not mean that processing in motor cortex is not influenced by factors not directly related to force output, like motor set. In this study the subject knew he had to make a response on one side but not on the other: response times are known to decrease as a result of this prior knowledge that allows for response selection. We find that reduction in beta power over motor cortex is a correlate of this response selection. Beta power over the decreases more motor cortex contralateral to the response side, thereby reflecting an expected functional involvement. The subject's set to respond only selectively modulates oscillatory neuronal synchrony in the period in which the go-cue can occur. This makes sense if beta power indeed corresponds to a mode in which the steady state is maintained; only in the period in which a response can be required this modus should be turned off to allow for dynamic changes in motor output.

The functional role of beta band synchrony

Oscillations in the beta band are an ubiquitous feature of human and nonhuman primate motor cortical areas and findings accumulate on the functional role of these oscillations. Beta band synchrony decreases before voluntary movement (Pfurtscheller, 1981), shows a rebound after movement (Pfurtscheller et al., 1996) and is strongly present during a steady contraction (Farmer, 1998). Although the role of beta synchrony has been compared to that of the alpha rhythm in visual cortex, that is thought to reflect cortical idling; this is probably too simple. Maintenance of balance is a highly active and demanding process that is normally accomplished without conscious thought. Recently, Gilbertson (2005) found that intrinsic fluctuations in the degree of beta band synchronization within the motor system were associated with a measurable impairment in movement performance in subjects. Their interpretation is that beta synchronization reflects a state in which the existing motor state is favoured at the cost of processing related to new movements. Beta band synchrony is also pathologically increased in Parkinson's disease (Schnitzler & Gross, 2005) and Parkinson patients have in particular difficulties with initiating movements. The benzodiazepine diazepam increases the size of GABAA IPSPs while the antagonist flumazenil has the reverse effect: Baker (2003) showed that EEG power in the beta band was greatly enhanced after diazepam injection and

returned to normal levels following flumazenil. In this experiment beta band activity was selectively reduced over the cortical area that was expected to be involved in responding to the go-cue. Beta band synchrony may act as a safety lock to maintain posture and balance. Reduction of this component may be an essential prerequisite for allowing efficient neural processing related to dynamic changes in motor output to take place. An area in a cortical state dominated by beta band synchrony is possibly less sensitive to small fluctuations of input and the current status can then be maintained with a minimum of computational effort. Motor set can selectively modulate the cortical state of a certain area to make it more responsive to changes in input. Doyle (2005) showed that lateralized EEG changes occur in the beta band only when informative warning cues allow early motor selection, as suggested by the shortened reaction times in that case. Thus, selective modulation can occur only as far as allowed by prior information. To conclude this section, evidence suggests that a reciprocal relationship exists between cortical beta activity and dynamic motor processing.

Reciprocal coupling of different bands

Instead of only looking at effects within a frequency band it is also possible to look at covariations among different frequencies (Friston, 1997). The general idea is that activity in lower frequency bands is reciprocally coupled to activity in higher frequency bands. Spatially restricted fast oscillations are thought to play an essential role in the formation of neuronal cell assemblies (Llinás et al., 2005). Therefore the disappearance of slow and extended oscillations in favour of oscillations that are faster and more localized is a signature of increased involvement in information processing. An example of this is found in visual cortex. In this experiment we confirmed the following result of the study by Hoogenboom (2006) who used a paradigm highly similar to ours: in the stimulation period gamma power was enhanced while alpha and beta power were reduced compared to baseline in occipital sensors with high signal-tonoise ratio. They found that this effect was found reliably across subjects and across multiple recording sessions of a given subject. Furthermore, the gamma power enhancement seemed to be more localized than the alpha power reduction. Thus, gamma power was increased in the period in which the visual stimulus was on and the subject expected the go-cue while power at lower frequencies was reduced. Tentatively, this reflects increased functional involvement and

reduced cortical idling. The reciprocal relation we observe between the power in the gamma and the alpha band in visual cortex is also thought to exist for the gamma and beta band in motor cortex. For example, the correlation with the readiness to respond is positive in the gamma band and negative in the beta band power over motor cortex (Schoffelen et al., 2005). Here we have shown directly that beta power over motor cortex goes down with motor set. We also show that the effect is lateralized giving bigger decreases over motor cortex contralateral to the side that needs to respond. The direct comparison between the stimulation period in condition left and condition right reveals a smaller power in the beta band over motor cortex when it needs to respond compared to when it needs to abstain from responding. Concluding, the power in the beta band seems to correspond to a mode of control suited to exerting constant force output. Importantly however, the amount of beta power can be modulated by cognitive factors such as motor set. This modulation is detectable during constant motor output. Gamma oscillations seem to come into play during dynamic changes or contraction with higher force (Brown, 2000). For instance, signal power in the gamma band in sensorimotor cortex is enhanced during performance of visuomotor tasks (Aoki, Fetz, Shupe, Lettich, & Ojemann, 1999). A consistent gamma band enhancement was not detected at the group level. The 1/f frequency drop-off inherent in biological signals, combined with measurement noise that is constant over frequencies, will lead to a worse signal to noise ratio for higher frequencies. The gamma band also compromises a bigger range on the frequency axis compared to lower frequencies. Both factors are unfavourable to group statistics that basically test the consistency of an effect. The fact that we did not find the effect in the gamma band could be the result of signal-tonoise or statistical issues we discussed or because it was not present. Reduction of synchrony in lower frequency bands and enhancement in higher bands could be modulated separately. In the stimulation period the subject needed to be ready but steady; one could already remove the safety lever (beta band reduction) of a gun when the command to fire is expected but not yet put his finger on the trigger (gamma band enhancement) to prevent premature acting.

Two different approaches provide cross-validation

Cluster analysis is an approach that makes no use of prior information about the location of the effect. Instead it gets its sensitivity from incorporating an assumption in the test statistic that is biophysically plausible, namely that effects at the sensor level are clustered in space and time. Cluster analysis can then reveal the most prominent effects in the entire sensor space. We note that a log transformation of the power spectra seems advisable in order to avoid that the high power of the MEG signal at lower frequencies dominates the signal. Corticomuscular coherence is modulated by task parameters (Kilner, Baker, Salenius, & Hari, 2000), but its functional role is still debated. We have shown how unilateral coherence in an independent data set can be used to select a group of channels that presumably represents motor cortex. This selection can subsequently be used as a starting point for the analysis of cortico-muscular and This cortico-cortical coherence. informed selection of a region of interest in advance reduces the multiple comparisons problem, simplifies data exploration and increases the power of the statistical test. The fact that the two different approaches reveal the same effects is supportive both for the effect as for the methods, providing cross-validation.

Stratification

In this experiment force output was required to stay within a narrow range so that subjects had to keep steady and controlled contractions. However, a difference in the point of applied force on the levers or a different pattern of co-activation of agonist and antagonist muscles could lead to the same force output with differences in EMG activity. These differences could in principle be systematically related to conditions. Stratification of the EMG resulted in a trial selection in which the distribution of the mean amplitude of the EMG left and the mean amplitude of the EMG right were not significantly different. Although this procedure reduced the number of trials in the analysis the difference between condition left and right remained present: with equivalent force output and equivalent EMG activity on both sides, beta power was lower over motor cortex when it was contralateral to the expected response side compared to when it was contralateral to the side that was not cued to respond.

Final conclusion

Oscillatory neuronal synchrony is likely to have a functional role in neural information processing. In the motor system a special role seems to be reserved for oscillations in the beta band in maintaining constant motor behaviour. A reduction in the dominance of beta power synchrony in motor cortex is then perhaps an essential prerequisite for allowing dynamic changes in motor output. Motor set can enhance the efficacy of motor behaviour by selective modulation of oscillatory synchrony in the beta band. We believe that future research on oscillatory network dynamics can bring us further towards a mechanistic understanding of cortical information processing

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