

1.6 The beta band

The beta band covers the frequencies from 15 to 26 Hz, and has a similar response to behavior and task demands as the motor-related alpha, or mu band activity. It has also been interpreted similarly, as an idling rhythm [187], although more recent studies suggest a more specific role [30]. Some differences between mu and beta band activity do exist, in terms of time course, location and the effects of manipulations, as will be described below.

1.6.1 Beta band activity during, after and preceding movement

Beta band activity decreases around responses over contralateral motor cortex, starting around 1.5 seconds prior to the onset of voluntary movements, recovering around one second post-movement, and subsequently overcompensating, with a peak at around two seconds post-movement [165] [220] [1]. This overcompensation is termed the beta rebound, and may be of special interest to a certain type of task switching, as described below. In the beta band, the rebound is more temporally localized, peaking and recovering more quickly, than in the mu band [165]; it also has a more anterior maximum [164]. Similarly to data showing alpha-band increases relative to baseline, the beta-band rebound suggests that such oscillations reflect a blocking of processing, as opposed to only its absence. As seen below, in vivo recordings show striatal increases in beta band activity during a movement task relative to rest, in contradiction to an interpretation of the beta band in terms of passive idling. Intracortical recordings from epilepsy patients show somewhat different effects of mu and beta activity in primary sensory and motor areas and the supplementary motor area (SMA) proper, preceding voluntary movements [174]. The SMA, being a more anterior prefrontal area than primary motor cortex, would be expected to be involved in organizing the brain in situations in which broad receptive fields in terms of time and content are needed. The SMA is sometimes termed the SMA proper to distinguish it from the pre-SMA; of these two, only the SMA proper has known corticocortical connectivity with primary motor and sensory cortices [175]. In primary areas, contralateral waveforms showed earlier pre-movement ERD than ipsilateral waveforms (around 1.5 versus 0.8 s), for both mu and beta bands but most clearly in the beta band. The mu and beta bands showed the strongest ERD in sensory and motor cortex, respectively. The difference between ipsilateral and contralateral ERD onset was not seen in the SMA proper, which showed a beta-band ERD starting 4 s pre-movement.

Using electrocorticogram data from epilepsy patients, movement-related coherence in the mu and beta band range was found between primary sensorimotor areas and the SMA [175]. In this study, partial coherence was used to avoid spurious coherence due to a common reference; a partializing electrode was used that showed no movement-related potentials. Subjects performed wrist or finger extensions, at 7 second intervals, and EMG onset was used to locate trials. Movement-related ERD and post-movement ERS, with a broad spread over frequencies centred around the beta band, was found in the primary motor and sensory areas and the SMA. The onset of ERD was earlier in the SMA (-1.8 s) than the primary regions (around -1.25 s). Mu-band coherence between the primary areas and the SMA proper was found, peaking at movement onset. Significant coherence, with a maximum in the beta band, was found between the pre-SMA and the primary sensory and motor cortices. The phase lag between coherent signals was near zero in more than half of the analyzed signal combinations.

1.6.2 Subcortical involvement in motor cortex beta activity

The cerebellar thalamus and the basal ganglia have been found to be related to cortical beta-band activity. In one study, a deep brain stimulation electrode was implanted in the cerebellar thalamus of patients with disorders of movement control (tremor and myoclonus), allowing scalp and thalamus measurements [177]. The cerebellar thalamus projects to primary motor cortex; see section 1.5.4 for a further description of thalamocortical interactions. The cerebellum itself receives input from climbing fibres and mossy fibres. Climbing fibres come from the inferior olive in the brain stem, which receives input from the cerebellum itself, spinal cord, brain stem and motor cortex. Mossy fibres project from the cerebellum itself, vestibular cells, the spinal cord, reticular formation, and basal pontine nuclei, which receive inputs from the neocortex. Lesions to the cerebellum cause motor corrections (that is, goal-directed adjustments based on the current motor state [133]) to be badly performed, leading to suggestions that the structure is necessary to transform a negative feedback signal into a corrective movement; this transformation, from a desired consequence to a motor action, is called an inverse model, as opposed to a forward model that would predict the consequences of a motor action [244]. In the implantation study, subjects performed self-paced wrist movements. Slow pre-movement potentials, starting two seconds before movement onset, were observed both on the scalp and in the thalamus. Scalp and thalamic alpha and beta band ERD were also found, with roughly 2.5 s pre-movement onsets except for a later thalamic alpha onset at 1.2 s prior to movement. Finally, a band of thalamus - scalp coherence was found around 20 Hz, that diminished around 0.5 s before movement onset. Thus, similar thalamocortical interactions may exist for the beta band and motor behavior as for the alpha band and perception.

Another study used electrodes surgically implanted in the subthalamic nucleus of patients with Parkinson's disease [242]. The subthalamic nucleus is part of the basal ganglia, a complex of structures that receives input from sources including sensory, motor and association cortices, the hippocampus, the limbic system, the thalamus and the cerebellum; and that outputs onto the thalamus, especially nuclei projecting to frontal cortex (section 1.3.2), lateral habenular nucleus and superior colliculus [242]. A possible role that has been suggested for the basal ganglia, based on its anatomical connectivity, is the learning of goal-directed disinhibition of transthalamic interactions [243]. In general agreement this idea, in Parkinson's disease, the basal ganglia degenerate and a rigidity has to be overcome to make voluntary movements. In the implantation study, patients performed a cued go - nogo task, in which a cue presented two seconds prior to the trigger stimulus was either informative as to the required movement (left or right responses) or not. For the informative (100 % valid) condition, beta-band ERS was seen just after (within 200 ms) cue presentation, followed by ERD up to around 0.5 s post-cue. In non-informative (50 % valid) blocks, only the post-cue ERD occurred. Thus, the basal ganglia contain cue-related beta-band activity. In an in vivo study of normal (non-Parkinsonian) monkeys, beta band activity in the local field potentials at sites in the caudate nucleus and putamen increased, relative to rest, during performance of an oculomotor task in which animals had to fixate on dots in a grid [41]. During rest, beta-band activity at different locations was highly synchronous. Task performance resulted in reduced beta-band amplitude and synchrony around saccades, starting around 100 ms before movement onset and ending around 100 ms after the saccade was completed. Thus, although over whole task blocks, beta activity was high relative to rest, the time course follows the idling prediction. Desynchronization (now literally, not as an interpretation of EEG amplitude) between regions was not global; sites could become desynchronized from a group of other sites, which did not show saccade-related

desynchronization. This study noted a technical issue that may have prevented such findings in earlier studies. Local field potentials measure the relatively slow post-synaptic effects of many spikes, from perhaps distant neurons, as opposed to individual spikes. Spike data may be less suited to detecting relatively global rhythmic activity. The beta-band activity was hypothesized to serve as a selective filter: only strong inputs to specific striatal modules could lead to their activity being distinguished from the global synchrony. The task-related increasing in amplitude would serve to make such break-throughs harder to achieve, and so facilitate a selective state, in this task, focussing on one specific point.

1.6.3 Cortex - muscle coherence

Axons from pyramidal cells in primary motor cortex descend to the the ventral horn of the spinal cord, from which spinal motoneurons project onto skeletal muscle fibres [34]. Despite the complex circuitry of the spinal cord itself, direct relations have been found between cortical (EEG) and muscle (electromyogram, EMG) activity. As described below, beta band activity has been found in electrical activity measured from muscles as it has been found in cortical signals, and beta-band coherence occurs between the cortical and muscle signals [202] [30].

In one study, subjects performed isometric contractions of finger, toe and foot muscles, and EEG - EMG coherence was studied [80]. As well as coherence, a time-dependent measure called phase synchronization was used, which measures the deviation of a set of phases' distribution from uniformity. Beta-band coherence between the EMG and contralateral primary motor cortex was found, as well as periodic bursts (which were themselves in the beta range) of beta-band phase synchronization time-locked to the onset of motor-unit potentials. Phase lags were found that were consistent with conduction times from motor cortex to the muscles (e.g. 15 ms for finger and 41 ms for toe muscles). It has been further shown that cortex - muscle coherence depends on the specific characteristics of movement demands [110]. The coherence was measured between MEG signals over left sensorimotor cortex and EMG's from the right arm, while subjects pressed together two levers in a precision grip task. Subjects had to pattern the force they exerted between finger and thumb, guided by visual feedback: first they held the lever at 1.3 N for 3 s; then they linearly increased the force, over 2 s, to 1.6 N, where that force was held for a further 3 s. Four conditions were created based on the stiffness versus compliance of the levers. More compliant levers had to be moved a longer distance to achieve the required force. Three levels of compliance were used, and an isometric condition in which the lever did not move at all. Over the whole task period, MEG and EMG power showed both mu and beta peaks, while MEG-EMG coherence showed a beta peak. Time-frequency analyses showed modulations of beta amplitude, which was highest during the hold periods of the task; this was not found in the mu band. Significant MEG - EMG coherence was found only during the hold periods, and, except for the isometric condition, was higher during the second period. The hold-period coherence increased with compliance. The same increase for the second hold period was found when grip force was increased in a jump, as opposed to over a ramp. The results show that beta-band activity and cortex - motoneuron communication are related to not allowing movement, as opposed to the absence of force production; and further that parameters of the system not to be moved influence the level of cortex - muscle coherence. A similar hold-specificity of beta-band EEG - EMG coherence was found in monkeys [13]. The monkeys were taught to perform a precision grip task, in which they held the position of levers between finger and thumb for around one second. Beta-band oscillations in local field potentials occurred once the hold position was reached, as well as beta-band coherence between cortical signals. Cortex - muscle

coherence was also found in the beta band, again during the hold portion of trials. The oscillatory activity was suggested to reflect a computationally robust neuronal state, suited to maintaining a motor state.

1.6.4 Beta band activity during motor imagery

The imagination of movement also affects beta-band activity [165]. Motor imagery, or action simulation, appears to rely on the same processes and structures as expressed in motor performance [98], see section 1.3.1. A 'resonance-like' [165] oscillation was affected by movements and imaging in an MEG study using sensory stimulation [206]. The median nerve of subjects' right arm was stimulated at 1 Hz, resulting in a somatosensory evoked field over the contralateral primary somatosensory cortex. Over primary motor cortex, during rest conditions, the stimulation caused a transient increase in beta-band activity, peaking at around 500 ms. This post-stimulus rebound was reduced by movements but also by the imagination of movements. This beta rebound was also suppressed during the observation of actions, in an MEG study in which subjects manipulated a small object or observed someone else, with their arm lying close to the subjects, manipulating the object [84]. Mu and beta band activity have been shown to respond somewhat differently to motor imagery, using the EEG [147]. Subjects either opened and closed the hand ipsilateral to a stimulus, or imagined doing so. During movements, mu and beta ERD were observed bilaterally, but most strongly contralateral to the movement. ERD was more focal in the mu band, over postcentral sites (CP3, CP4) close to somatosensory cortex. The same pattern, although with smaller ERDs relative to rest, was found for imagery. Left - right differences in the mu band were as strong for imagery as actual movements. Such results, together with data showing pre-movement ERD as described above, involve beta-band activity in the WwM framework of section 1.3.1.

1.6.5 Motor-related rhythmic activity and task switching

Motor-related beta-band activity may be relevant to task switching in a number of ways. First, such activity may be involved with destroying part of a previous task set. Task switching is associated with motor-related effects: the diminishment of response repetition benefits [197] and the prolongation of the LRP-R interval [92]. As, further, switch costs are caused by obsolete stimulus - response associations, cognitive control aimed at reducing switch costs may change the conditions for giving responses. That is, task-set reconfiguration may not involve (only) the route from stimulus to response, but the feedback involved in controlled responding: is the response achieving the correct goal? Such a change, since task sets have stability [3], requires energy to break through the old attractor. Mu- and beta-band ERS appear to be worth studying as hypothetical sources of this energy. The imagery results already show that motor-related ERS is under intentional control. So, if the brain cancels response-related states by modulating motor-related ERS, this should be observable during task switching, especially during intentional switches (i.e. response remapping) [200].

Second, the reverse pattern could occur: preparation for a new task could involve motor-related ERD. If this is the case, it would suggest that the control involved in task switching is more interested in setting up the new task than tearing down the previous one. These first two processes could also take place in sequence, ERD following ERS as the path is cleared for the new task set.

Third, if tasks differ on response effector, switching tasks becomes equal to changing the bias between the effectors. If either the right or the left hand is used, a switch to the right-hand task

could be achieved by putting the left hand into a hold state, which would be visible in beta-band EMG-EEG coherence.

Finally, the beta ERS following responses may be part of the reason why switch costs are mostly confined to a single trial. At a muscular level, beta band activity is associated with a holding pattern; perhaps something similar is the case cortically, so that once a response is given, the preceding task set is stabilized. If this is the case, faster responses should be seen following higher beta ERS for hold trials, but the reverse should be the case for switch trials.