CHAPTER 2

The cortical activation model (CAM)

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Abstract: The Cortical Activation Model (CAM) is an attempt to explain whether an internally or externally paced event reveals an event-related desynchronization (ERD) or event-related synchronization (ERS) in a specific frequency band. It is assumed that the amplitude of network-specific oscillations depends on, in addition to other factors, the number of neurons available for synchronization and the excitability level of neurons and forms a bell-shaped curve with a maximum of oscillatory activity at a certain balance of both factors. Depending on the baseline level of cortical activation (CA) and the location of the "working point" (WP), a sudden change of activation can induce either ERD or ERS in a given area.

Introduction

One important feature of the brain is its ability to generate characteristic rhythms in cortical regions. Already in Jasper and Penfield (1949) discovered this fact and discussed the relationship between alpha and beta rhythms and their functional importance in relation to the underlying neural networks. The frequency of brain oscillations depends both on the membrane properties of single neurons and on the organization and interconnectivity of networks to which they belong (Lopes da Silva, 1991). Such networks comprises either a large number of neurons controlled by thalamo-cortical feedback loops or only a small number of neurons interconnected by intra-cortical feedback loops. Coherent activity in large neuronal networks can result in high-amplitude and low-frequency oscillations (e.g., alpha-band rhythms), whereas synchrony in localized neuronal networks can be the source of lower amplitude higher frequency

(gamma) oscillations (Lopes da Silva and Pfurtscheller, 1999). The activation/deactivation of such networks can result in phasic changes in the synchrony of cell populations due to externally or internally paced events and can lead to characteristic EEG patterns. Two such pattern types are observed: event-related desynchronization (ERD), which is defined by amplitude attenuation; and event-related synchronization (ERS), which is characterized by an enhancement of specific frequency components (Pfurtscheller and Lopes da Silva, 1999a). It is important to note that both ERD and ERS are highly frequency-band specific. So, for example, induced gamma bursts (e.g., 40-Hz ERS) have to do with binding, feature linking, and sensorimotor integration (Singer, 1993) and represent a network response associated with cortical activation (CA). Alpha desynchronization (e.g., 10-Hz ERD) is a reliable correlate of increased neuronal excitability in thalamo-cortical systems (Steriade and Llinas, 1988) and therefore also characteristic for CA. Whereas ERD is typically observed in alpha and lower beta bands, ERS is found in alpha, beta, and gamma bands.

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Relation between ERD/ERS and CA

Speckmann and Caspers (1973) found that the amplitude response of a complex neuronal system depends on the number of neurons available and therefore "unoccupied" at the time of stimulation and their level of facilitation. Therefore, we conclude that neuronal networks can display different states of synchrony, whereby the amplitude of oscillatory activity generated by such a network depends on, in addition to a number of other factors, e.g. ionic and synaptic activities, on the number of neurons available for synchronization and the excitability level of cortical neuronal populations (Fig. 1). Referring to Fig. 1, it is assumed that the amplitude of frequency-specific oscillations can form something like a bell-shaped curve (there exists, however, no experimental evidence for this) dependent on the excitability level of neurons and the availability of neurons for synchronization with a maximum at a certain balance between availability and excitability level. When the baseline level of CA is low and most of the neurons in a given area are still available for synchronization an ERS is expected during CA increase. In the case, when the CA baseline level is high and the majority of neurons is occupied by synchronization

processes an increase of CA can only induce an ERD. The number of neurons available for synchronization and the excitation level of cortical neurons are the two parameters that define the amplitude of oscillations and therewith the working point (WP) on the bell-shaped curve in the Cortical Activation Model (CAM).

ERD/ERS depends on the level of consciousness

Oscillations in the alpha band can display either ERD or ERS depending on the level of consciousness. This was supported by a follow-up study in a comatose patient with a brainstem hemorrhage, where visual stimuli were applied in deep coma (starting with Glasgow Coma Scale, GCS = 4) and after recovery from coma (GCS = 15). In the first case, visual stimuli induced bursts of oscillations (ERS), while in the second case, the same physical stimulus resulted in an ERD (Pfurtscheller, 1992). Induced spindle activity (ERS) during unconsciousness in sleep or coma is associated with a blockade of information transmission from the thalamus to the cortex (Steriade and Llinas, 1988; Lopes da Silva, 1991) and reflects decreased intra-cortical processing. The transition from the deep
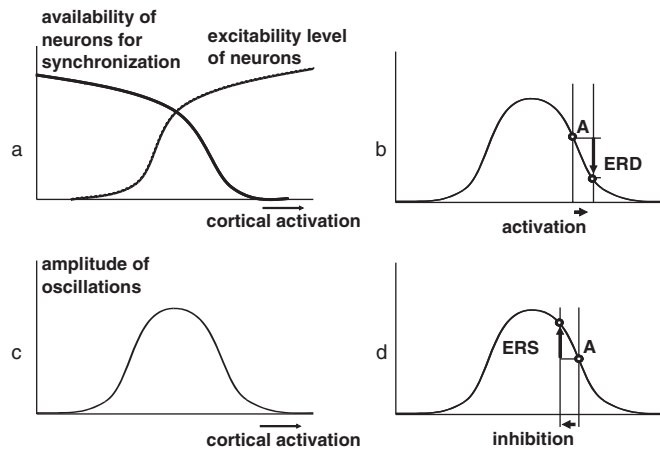

Fig. 1. Strongly simplified diagram displaying the relationship between cortical activation (CA) (horizontal axis), excitability level of neurons (right vertical axis), and availability of neurons for synchronization (left vertical axis) (a). From diagram (a) results the strongly simplified relationship between CA and amplitude of oscillations in a specific frequency band in form of a bell-shaped curve (b). The network response (ERD or ERS) depends on the baseline level of CA at the time-point of an externally or internally paced event. At a certain baseline level of CA (working point A) an increase of CA results in an ERD (c) whereas a decrease of CA (inhibition) induces ERS (d).

comatose state to an awakened state is accompanied by a dramatic increase of the CA level and can be documented by a shift of the WP in the CAM from "A" to "B" (Fig. 2). That is, stimulation results in an ERS at WP location "A" whereas an ERD is characteristic for WP "B".

Simultaneous occurrence of ERD and ERS at one cortical location

A cortical area is composed of different networks and can therefore generate a variety of oscillations in the alpha, beta, and gamma bands. For example, an interaction between alpha and gamma band oscillations in sensorimotor areas exists in such a way that gamma bursts are very often embedded in desynchronized or blocked alpha waves. Such a simultaneous occurrence of both alpha ERD and gamma ERS in single recordings of EEG and electrocorticography (ECoG) in a movement task has been reported by several researchers (Pfurtscheller and Neuper, 1992; Crone et al., 1998; Pfurtscheller et al., 2003a). Crone et al. (1998) observed widespread alpha power suppression at the onset of sustained muscle contractions in different body parts and a more discrete gamma power augmentation that was more

somatotopically specific for body parts. Pfurtscheller and Neuper (1992) reported on 40-Hz gamma bursts simultaneously with a mu ERD in contralateral EEG recordings during pressing of a micro switch with the right index finger. Transferring these observations to the CAM means that in the case of desynchronized alpha oscillations, the WP is on the declining right part of the bell-shaped curve, while in the case of induced gamma oscillations, the WP is located on the rising left part of the curve. In the case of oscillations in different frequency bands, however, we have to deal with two different CAMs corresponding to two different network properties (Fig. 3).

Task-dependent occurrence of ERD or ERS at the same cortical locations

An interesting observation is the antagonistic behavior of rhythms in motor and visual areas. Visual stimulation results in the classical blocking or desynchronization of occipital alpha rhythms but can also enhance the central mu rhythm at the same time (Brechet and Lecasable, 1965; Koshino and Niedermeyer, 1975). On the contrary, an enhancement of occipital alpha rhythms and desynchronization of central mu rhythms is
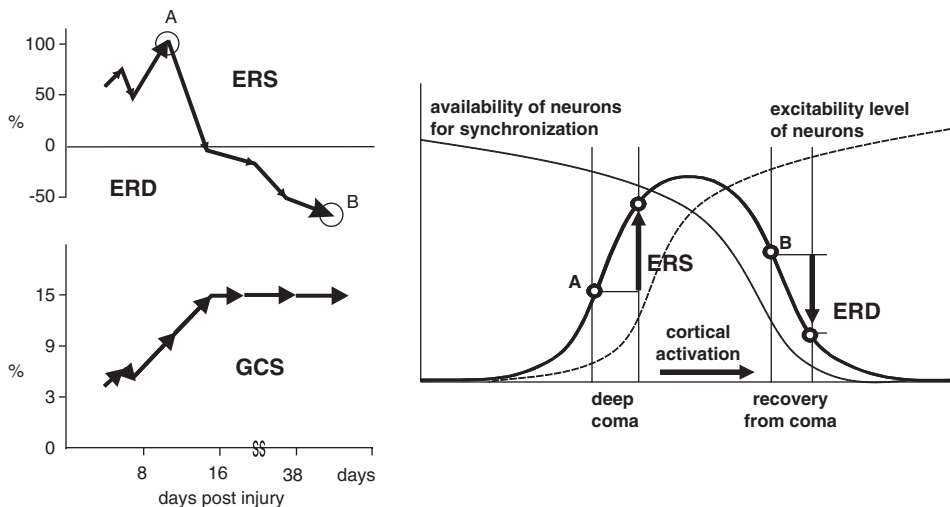
Fig. 2. Data from a 20-year-old patient during recovery from a brainstem hemorrhage. Displayed are follow-up measurements of ERD/ERS in the 6–14 Hz band during recovery from coma. The coma is evaluated by the Glasgow Coma Scale (GCS). Two measurements (one with ERS and one with ERD) are indicated in the CAM. Modified from Pfurtscheller (1992).
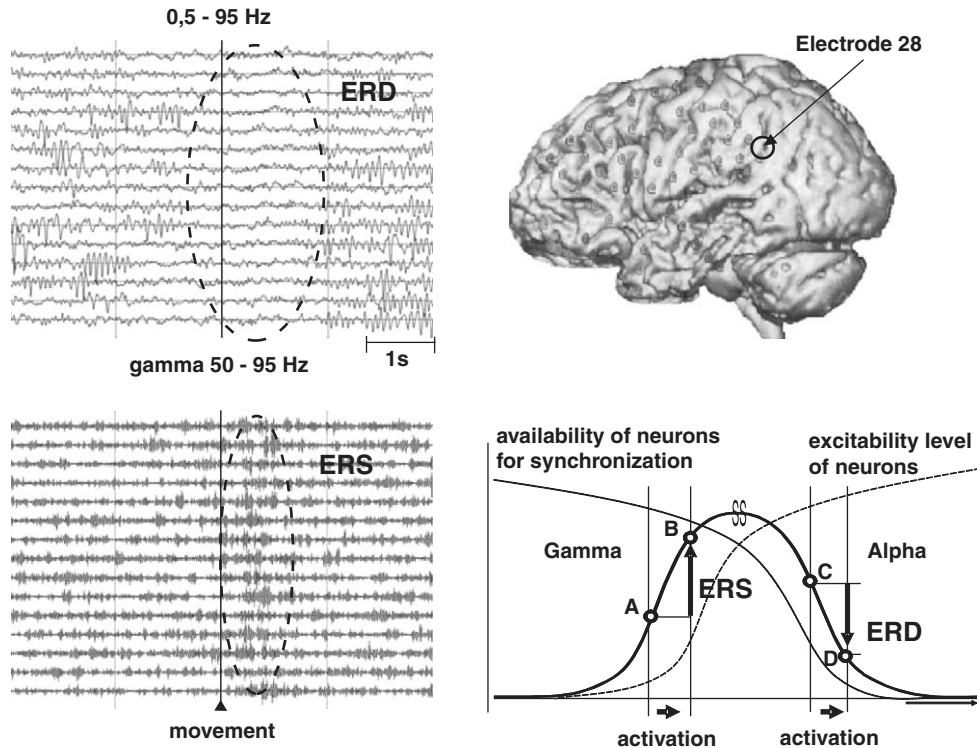
Fig. 3. Example of electrocorticography (ECoG) data recorded synchronously to hand movement in a candidate for epileptic surgery. The location of the electrode is marked on the reconstructed brain image. The long-lasting ERD in the row ECoG data is clearly visible as is the embedded short-lasting ERS in the band filtered (50–95 Hz) trials. Both phenomena, ERD and ERS, correspond to a CA and are indicated in the CAM. Modified from Pfurtscheller and Lopes da Silva (2005).

characteristic for a motor task (Kreitmann and Shaw, 1965; Pfurtscheller, 1992; Gerloff et al., 1998). Such an antagonistic behavior can be observed not only in different modalities but also within the same modality. One example of the latter is the interaction between different sensorimotor areas in a motor task where ERD and ERS can be observed in the same recording at the hand representation area (electrode position C3 or C4) depending only on the type of motor behavior. Execution of hand/finger movement or imagination of the same movement (for review see Pfurtscheller and Lopes da Silva, 1999b) is characterized by a focused ERD in the hand area, whereas execution or imagination of foot movement can reveal an ERS in the hand area (Pfurtscheller et al., 2006). An example of the latter is given in Fig. 4, which shows row EEG trials with the corresponding topographic map and the

band power time course for the 11–13 Hz band. The induced ERS is indicated in the CAM. Evidence that similar networks are involved in motor execution and motor imagery comes from functional magnetic resonance imaging (fMRI) (see, e.g., Lotze et al., 1999).

A decrease of regional cerebral blood flow (rCBF) measured by PET was reported in the primary somatosensory cortex outside of the representation of the skin area that was the target of the expected stimulus (Drevets et al., 1995). This can be interpreted that attention focused to one body part (e.g., area for toe) results in an rCBF decrease in other non-attended body parts (e.g., areas for finger and face). Transferring these findings to the motor imagery task means that focused attention to a foot movement task (either executed or imagined) should be accompanied by a simultaneous withdrawal of attention from the hand area and
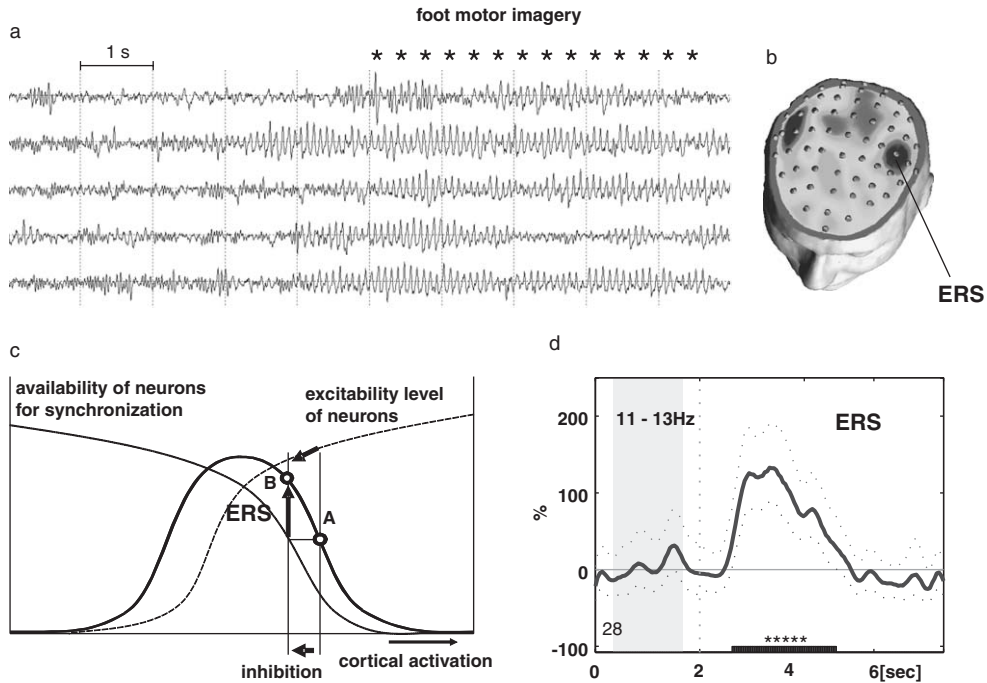
foot motor imagery

Fig. 4. Induction of ERS in the hand representation area during foot motor imagery. Displayed are row EEG trials, mean band power change in the 11–13 Hz band with dominant ERS, and topographic map with ERS-foci over both hand representation areas and the representation of the ERS in the CAM.

reinforce the cooperative behavior of neurons in the hand area resulting in an enhancement of the hand area mu rhythm. The hand area mu ERS as reported not only during foot and tongue motor imagery (Pfurtscheller et al., 2006) but also during foot and tongue movement (Pfurtscheller and Neuper, 1994), can be interpreted, therefore, as a correlate of inhibited neuronal structures in the hand representation area corresponding to a shift of the WP to the left side in the CAM.

Further support for the concurrent existence of activation and inhibition of cortical networks came from the work of Hummel et al. (2002). They investigated context-dependent modulation of motor memory traces with ERD/ERS quantification and transcranial magnetic stimulation (TMS) over the primary motor cortex. During active retrieval of the motor memory trace (activation condition), the motor evoked potentials (MEPs) were increased and oscillations in the frequency range of 11–13 Hz showed an ERD. In the inhibition condition, the MEPs displayed a significant amplitude decrease compared with the baseline and the oscillations between 11 and 13 Hz showed a significant increase (ERS). Hummel et al. (2002) proposed that the focal ERS in a given area is instrumental for inhibitory control at the cortical level. It is of interest to note that similar frequency components around 12 Hz are enhanced (ERS) in the hand area when a subject performs foot or tongue motor imagery (Pfurtscheller et al., 2006). Therefore, enhanced 11–13 Hz mu components in the hand representation area can be seen as an expression of an inhibited network with reduced intra-cortical processing.

Beta ERS as marker for the CA level

A very interesting brain phenomenon is the short-lasting bursts of oscillations in the beta band following somatosensory stimulation, motor execution, or motor imagery (Neuper and Pfurtscheller, 2001a; Pfurtscheller et al., 2005). This beta ERS,
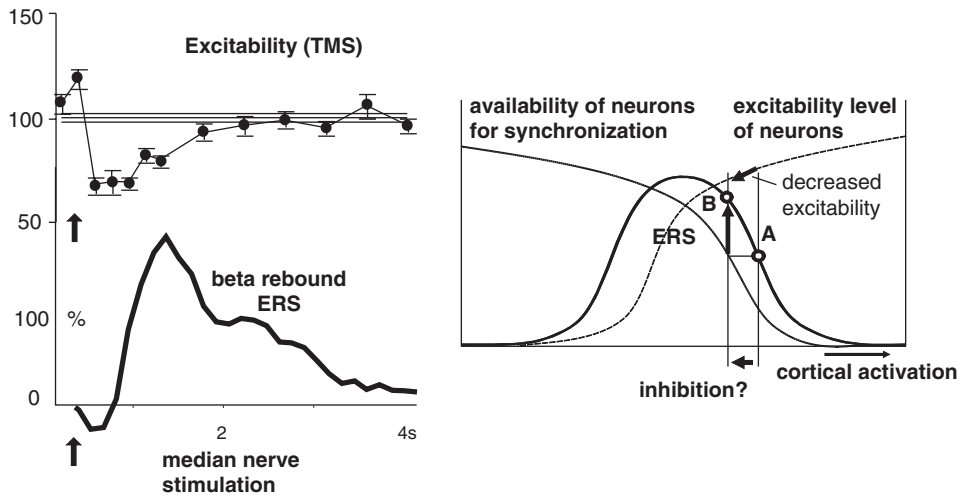
Fig. 5. Example of cortical excitability time course after median nerve stimulation measured by TMS (Chen et al., 1998) and time course of beta-band power changes (Neuper and Pfurtscheller, 2001b). Both the reduction of the cortical excitability and the beta rebound (beta ERS) are marked in the CAM and indicative for inhibition of motor cortex networks.
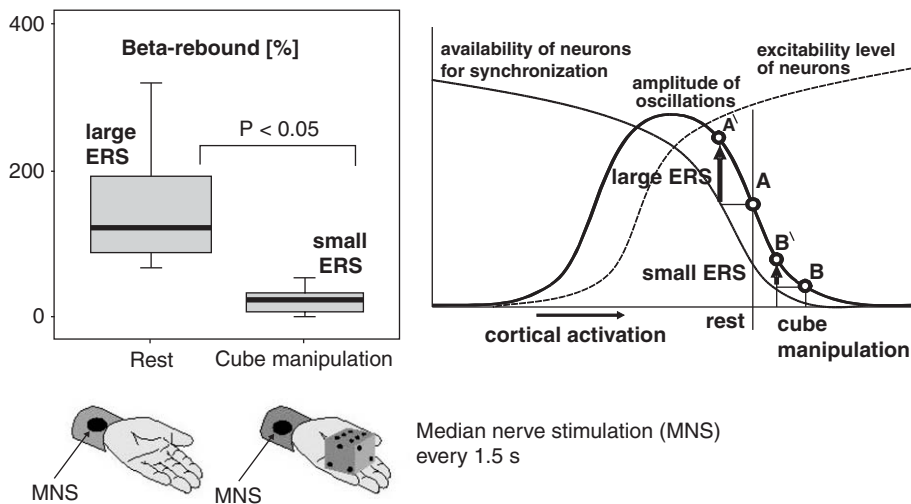

Fig. 6. Effect of CA through complex hand movement on the stimulation-induced beta rebound with a large beta rebound during rest and a nearly suppressed beta rebound during cube manipulation. The data are from eight subjects. The two different brain states (rest, complex movement) are represented by two WPs on the CAM. Modified from Pfurtscheller et al. (2002).

known as beta rebound or post-movement beta synchronization (Cassim et al., 2001), shares some interesting features: strict somatotopic organization (Salmelin et al., 1995), similar patterns with active and passive movement (Cassim et al., 2001) and after somatosensory stimulation (Neuper and Pfurtscheller, 2001). Of special interest is the observation that the beta rebound coincides with a reduced excitability of motor cortex neurons as studied by TMS during hand movement and median nerve stimulation (Chen et al., 1998, 1999). The results revealed a period of decreased corticospinal excitability after movement offset and stimulation, respectively. This period lasting about 1 s corresponds to the occurrence of the beta rebound (beta ERS) (Fig. 5).

An interesting and important observation is the suppression of the induced beta rebound (beta ERS) during manipulatory finger movements in MEG (Schnitzler et al., 1997) and EEG data (Pfurtscheller et al., 2002). The beta ERS is attenuated with respect to the baseline level not only during complex finger movements but also during imagination of manipulatory movements (Schnitzler et al., 1997). If the beta ERS is a correlate of decreased cortical excitability, an attenuated or suppressed ERS is expected during CA, as for example during manipulatory or complex finger movements. In this case, the overall cortical excitability level is increased and compensates the transient excitability decrease after termination of a motor task. Therefore, the beta ERS can be seen as a marker of the CA level, with a large magnitude during the resting state and a small or suppressed magnitude during activation of cortical structures, as in the case of manipulatory finger movements. An example of increased CA during finger movement compared with the rest condition (baseline level) is illustrated in Fig. 6 by a transition of the WP from A to B. In the former case (WP "A"), the ERS is of large amplitude, whereas in the latter case, the ERS is nearly suppressed. Data from a real experiment are reported in Fig. 6, left side (Pfurtscheller et al., 2002).

Conclusion

Cortical (de)activation can be assessed by different methods such as ERD/ERS quantification in the EEG, TMS, and fMRI. Activated cortical areas involved in a motor task are characterized by decreased alpha (mu) oscillations (ERD) (Pfurtscheller and Lopes da Silva, 1999a) and increased responses to TMS and a positive BOLD signal (Logothetis et al., 2001; Hummel et al., 2002, 2004; Rau et al., 2003), and corresponds to a right-side shift in the CAM. Deactivation (removal of excitation back to baseline level) or inhibition (below baseline level) of networks in the sensorimotor cortex can be accompanied by a decreased response to TMS (Chen et al., 1999; Hummel et al., 2002), a reduced rCBF (Drevets et al., 1995), and a negative BOLD signal (Hummel et al., 2004). Such

a deactivation or inhibition is always reflected in the CAM by a left-side shift together with a mu or beta ERS. Characteristic for the mu ERS is the narrow-banded enhancement of components around 12/13 Hz (Hummel et al., 2002; Pfurtscheller et al., 2006). Such a narrow-banded mu ERS was reported not only in the hand area after foot or tongue motor imagery or during a motor memory inhibition condition but also in the ipsilateral hand representation area during execution of finger movements (Pfurtscheller and Neuper, 1992) or during hand motor imagery (Pfurtscheller and Neuper, 1997). In the latter cases, we can suppose that this focal hand area ERS is an indicator for an inhibiting process in the ipsilateral hand area not directly involved in the motor task and perhaps helps to shape the activation of networks on the contralateral side.

The CAM can help to predict the occurrence of ERD or ERS dependent on the frequency band investigated and the baseline level of CA. Both alpha (mu) ERD and gamma ERS are characteristic examples of neuronal responses associated with activation processes and increased information processing. In the former case, the WP is represented on the right side of the bell-shaped curve, in the latter case on the left side. In the case of beta oscillations (<35 Hz) the WP in the CAM can be located, however, either on the left or right side of the maximum of the bell-shaped curve. CA can therefore reveal beta synchronization or desynchronization. Beta ERD is very often found in parallel with mu ERD in a motor task (for review see Pfurtscheller et al., 1999) and is represented by a WP on the right side, similar as characteristic for alpha (mu) oscillations (Fig. 1). In addition to the beta ERD also a beta ERS can be a signature of a CA process. So, for example, a stable and reproducible beta ERS was reported during foot motor imagery in a tetraplegic patient (Pfurtscheller et al., 2003b). This beta ERS was the result of a large number of BCI training sessions where the patient focused his attention over and over to the foot representation area through foot motor imagery. After some months of training, suddenly 17-Hz beta oscillations were induced close to electrode positions near the vertex. Because of this focused beta ERS at the vertex, we can suppose that

structures in the foot representation area and/or the supplementary motor area (SMA) were activated during motor imagery and, as a consequence, neurons became synchronized. It is speculated that these induced 17-Hz beta oscillations in the tetraplegic patient are a type of slowed gamma oscillations, associated with sensorimotor integration processes in cortical areas that are affected by the spinal cord injury.

Localized desynchronization of alpha and beta band activity (ERD) related to a specific event does not occur in isolation, but is very often accompanied by an increase of synchronization in neighboring cortical areas that correspond to the same or to another modality. To describe this observation the term "focal ERD/surround ERS" was introduced by Prof. Lopes da Silva (Suffczynski et al., 1999). An example of this kind of intramodal interaction is displayed in Fig. 4. The antagonistic ERD/ERS pattern is accounted for by the interactions between thalamo-cortical modules due to changes of "lateral inhibition within a network in inhibitory neurons". The fact that in one active module the degree of inhibition decreases due to a specific activation (focal ERD) leads to the removal of inhibition on the inhibitory network (disinhibition) of the neighboring modules (surround ERS) (Suffczynski et al., 2001). It has to be noted, however, that this type of modular inhibition is on the level of a macro scale whereas the inhibition displayed in the CAM is on a regional scale and associated with a decreased cortical excitability level (Chen et al., 1999; Hummel et al., 2002; Rau et al., 2003).

The ERD/ERS pattern is interpreted as a thalamo-cortical mechanism to facilitate focal activation and information processing (focal ERD) by simultaneous deactivation or inhibition of other cortical areas (surround ERS) with the goal to optimize the energetical demand in task-related cortical areas.

Acknowledgments

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