Invited review

Event-related EEG/MEG synchronization and desynchronization: basic principles

G. Pfurtscheller[a,*], F.H. Lopes da Silva[b]

[a]*Department of Medical Informatics, Institute of Biomedical Engineering, Technical University Graz, Inffeldgasse 16a/II, A-8010 Graz, Austria*
[b]*Institute of Neurobiology, Faculty of Biology, Graduate School of Neurosciences, Amsterdam, The Netherlands*

Abstract

An internally or externally paced event results not only in the generation of an event-related potential (ERP) but also in a change in the ongoing EEG/MEG in form of an event-related desynchronization (ERD) or event-related synchronization (ERS). The ERP on the one side and the ERD/ERS on the other side are different responses of neuronal structures in the brain. While the former is phase-locked, the latter is not phase-locked to the event. The most important difference between both phenomena is that the ERD/ERS is highly frequency band-specific, whereby either the same or different locations on the scalp can display ERD and ERS simultaneously. Quantification of ERD/ERS in time and space is demonstrated on data from a number of movement experiments. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

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1. Event-related potentials/fields vs. event-related EEG/MEG changes (ERD/ERS)

Several kinds of events, the most notably being sensory stimuli, can induce time-locked changes in the activity of neuronal populations that are generally called event-related potentials (ERPs). In order to detect such ERPs, averaging techniques are commonly used. The basic assumption is that the evoked activity, or signal of interest, has a more or less fixed time-delay to the stimulus, while the ongoing EEG/MEG activity behaves as additive noise. The averaging procedure will enhance the signal-to-noise ratio. However, this simple and widely used model is just an approximation of the real situation. Indeed it is known that evoked potentials (EPs) can be considered to result from a reorganization of the phases of the ongoing EEG signals (Sayers et al., 1974). In addition it was also shown that visual stimuli can reduce the amplitude of the ongoing EEG amplitude (Vijn et al., 1991), thus demonstrating that the model assuming that an ERP can be represented by a signal added to uncorrelated noise does not hold in general. Furthermore, it is known since Berger (1930) that certain events can block or desynchronize the ongoing alpha activity. These types of changes are time-locked to the event but not phase-locked,

and thus cannot be extracted by a simple linear method, such as averaging, but may be detected by frequency analysis. This means that these event-related phenomena represent frequency specific changes of the ongoing EEG activity and may consist, in general terms, either of decreases or of increases of power in given frequency bands. This may be considered to be due to a decrease or an increase in synchrony of the underlying neuronal populations, respectively. The former case is called event-related desynchronization or ERD (Pfurtscheller, 1977; Pfurtscheller and Aranibar, 1977), and the latter event-related synchronization (ERS) (Pfurtscheller, 1992). Of course ERD and ERS phenomena are not only found with EEG but also with MEG recordings.

In contrast with the traditional ERPs that can be considered as a series of transient post-synaptic responses of main pyramidal neurons triggered by a specific stimulus, ERD/ERS phenomena can be viewed as generated by changes in one or more parameters that control oscillations in neuronal networks (Fig. 1). We should indicate briefly which are the general properties of such oscillations. Two kinds of factors determine the properties of EEG oscillations (Lopes da Silva, 1991; Singer, 1993):

1. the intrinsic membrane properties of the neurons and the dynamics of synaptic processes;
2. the strength and extent of the interconnections between the network elements, most often formed by feedback
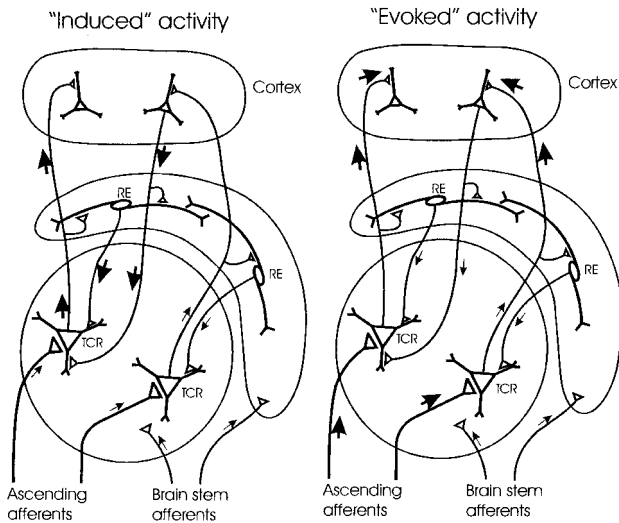
Fig. 1. Schema for the generation of induced (ERD/ERS) and evoked (ERP) activity whereby the former is highly frequency-specific. TCR thalamic relay cells; RE reticular thalamic nucleus.

loops. Different kinds of feedback loops can be distinguished:, involving thalamo-cortical or cortico-cortical either at short or at long distances;

3. the modulating influences from general or local neurotransmitter systems.

Neuronal networks can display different states of synchrony, with oscillations at different frequencies. Indeed we found (Lopes da Silva et al., 1970; Lopes da Silva, 1991) that from the same cortical areas in dog, alpha rhythms or beta/gamma activities could be recorded, the former when the animal was quietly awake with eyes closed and the latter when it was paying attention to a visual screen expecting a stimulus that would indicate a food reward. The former rhythmic activity was common all over the visual cortex and corresponding thalamic nucleus, while the latter was much more variable, both in space and frequency. When the neuronal populations display resonant behavior, i.e. they present oscillations, the latter tend to recruit neurons in larger cortical areas in the case of low frequencies, as in the previous example for the alpha rhythm, and to be more spatially restricted in the case of higher frequencies, as for beta/gamma rhythms. In the latter case, the cortex appears to be functionally organized as a mosaic of neuronal assemblies characterized by relatively high frequency synchronous oscillations that may display a large variability in dominant frequencies. In short, we may assume that ERPs represent the responses of cortical neurons due to changes in afferent activity, while ERD/ERS reflect changes in the activity of local interactions between main neurons and interneurons that control the frequency components of the ongoing EEG.

For the research with ERD/ERS it is recommended:

1. when referring to ERD/ERS of the EEG/MEG it is necessary to specify the frequency band;

2. the term ERD is only meaningful if the baseline measured some seconds before the event represents a rhythmicity seen as a clear peak in the power spectrum. Similarly, the term ERS only has a meaning if the event results in the appearance of a rhythmic component and therewith in a spectral peak that was initially not detectable (Lopes da Silva and Pfurtscheller, 1999).

2. Frequency-specificity of brain oscillations

In general, the frequency of brain oscillations is negatively correlated with their amplitude, which means that the amplitude of fluctuations decreases with increasing frequency. For example, the Rolandic mu rhythm with a frequency between 8 and 13 Hz has a larger amplitude than the central beta rhythm with frequencies around 20 Hz. The beta rhythm again has a larger amplitude than oscillations around 40 Hz. Because the amplitude of oscillations is proportional to the number of synchronously active neural elements (Elul, 1972), slowly oscillating cell assemblies comprise more neurons than fast oscillating cells (Singer, 1993). This is valid not only when comparing oscillations around 10, 20 and 40 Hz but also for components within the individual frequency bands. A simulation study performed by Lopes da Silva et al. (1976) can help to explain the relationship between amplitude and frequency of brain oscillations (Fig. 2). With an increasing number of interconnecting neurons and therewith an increasing number of coherently activated neurons, the amplitude increases and the frequency decreases. The lower alpha component in Fig. 2 has a larger spectral peak magnitude than the higher alpha component. For further details see also Lopes da Silva and Pfurtscheller (1999) and Pfurtscheller and Lopes da Silva (1999).
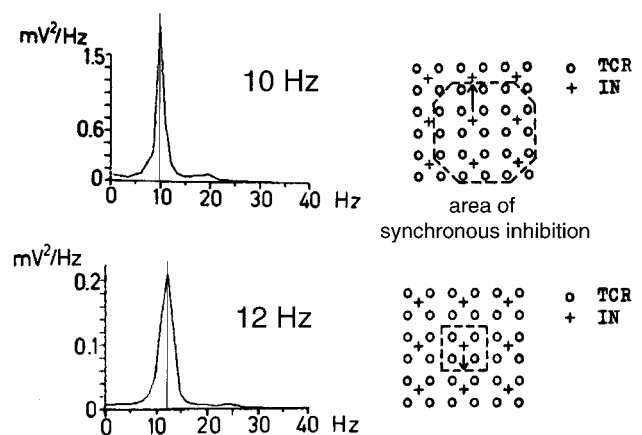

Fig. 2. Results of a simulation study displaying the relationship between frequency and interconnectivity of neurons. The area of synchronous inhibition is marked. TCR thalamic relay cells; IN interneurons, (modified from Lopes da Silva et al., 1976).

Table 1
Quantification of ERD/ERS in the time domain used in different labs. (Modified fromPfurtscheller et al., 1999)

ERD quantification method	References
Band power method	Pfurtscheller and Aranibar (1979); Boiten et al. (1992); Dujardin et al. (1993); Klimesch et al. (1994); Toro et al. (1994); Aftanas et al. (1996); Defebvre et al. (1996); Krause et al. (1996); Sterman et al. (1996); Zhuang et al. (1997); Magnani et al. (1998)
Intertrial variance method	Kalcher and Pfurtscheller (1995); Klimesch et al. (1998)
Autoregressive models and spectral decomposition	Florian and Pfurtscheller (1995)
Hilbert transformation	Burgess and Gruzelier (1996); Clochon et al. (1996)
Complex demodulation	Nogawa et al. (1976)
Temporal-spectral evolution method (TSE)	Salmelin et al. (1995)
Event-related spectral pertubation (ERSP)	Makeig (1993); Wei et al. (1998)
Task-related power increase (TRPI), task-related power decrease (TRPD)	Gerloff et al. (1998)

3. Quantification of ERD/ERS in time and space

3.1. Time course of ERD/ERS

One of the basic features of ERD/ERS measurements is that the EEG/MEG power within identified frequency bands is displayed relative (as percentage) to the power of the same EEG/MEG derivations recorded during the reference or baseline period a few seconds before the event occurs. Because event-related changes in ongoing EEG/MEG need time to develop and to recover, especially when alpha band rhythms are involved, the interval between two consecutive events should last at least some seconds. In the case of voluntary limb movement studies, an inter-event-interval of at least approximately 10 s is recommended; in the case of a foreperiod reaction time task, the interval should be even longer.

The classical method to compute the time course of ERD includes the following steps:

1. bandpass filtering of all event-related trials;
2. squaring of the amplitude samples to obtain power samples;
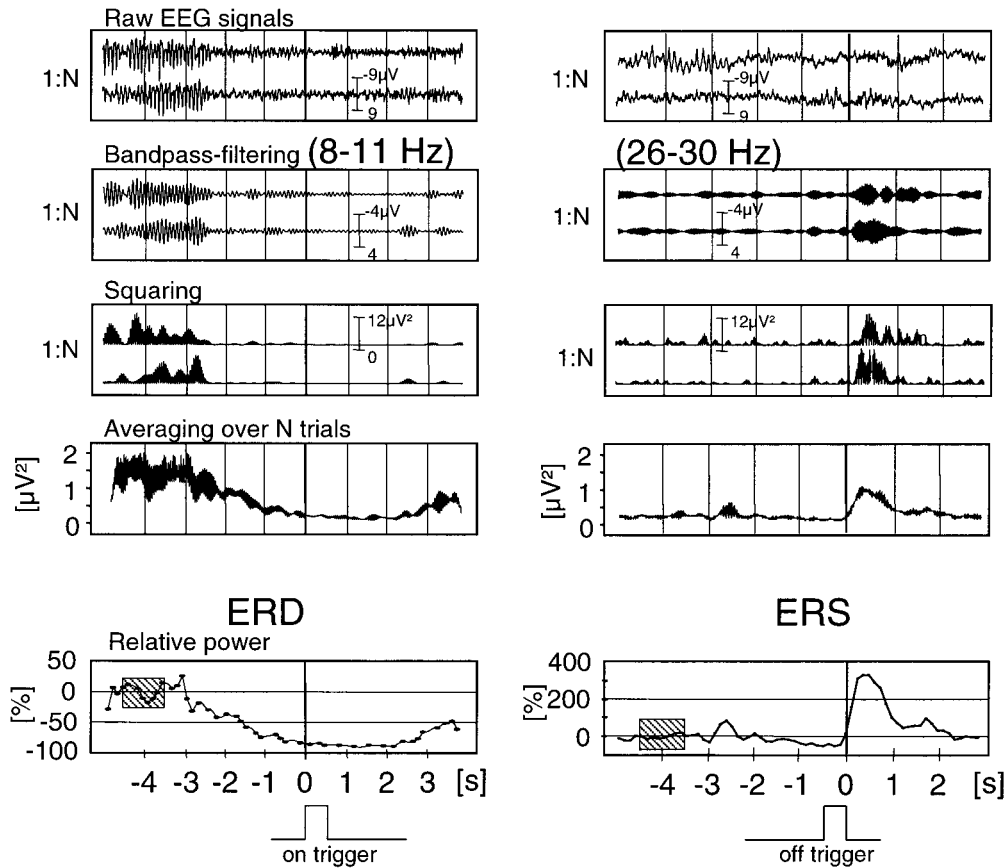3. averaging of power samples across all trials;

Fig. 3. Principle of ERD (left panel) and ERS (right panel) processing. A decrease of band power indicates ERD and an increase of band power ERS. Note the different triggering with ERD and ERS processing (modified from Pfurtscheller, 1999).

Table 2
Methods for mapping of EEG/MEG parameters (modified from van Burik et al., 1999)

Method	Reference
Surface Laplacian	
Source derivation	Hjorth (1975)
Local average reference	Thickbroom et al. (1984)
Local estimate on realistic surface	Huiskamp (1991); Le et al. (1994)
Spherical splines	Perrin et al. (1987)
3d Splines on spherical and ellipsoidal surface	Law et al. (1993)
3d Splines on realistic surface	Babiloni et al. (1996)
Cortical imaging	
Spherical volume conductor	Kearfott et al. (1991); Edlinger et al. (1998)
Realistic head model, FEM	Gevins et al. (1991)
Distributed source imaging	
First introduction for MEG	Hämäläinen and Ilmoniemi (1984)
Applied to spontaneous MEG	Wang et al. (1993)
Applied for ERD/ERS analysis	van Burik et al. (1998); van Burik and Pfurtscheller (1999)

4. averaging over time samples to smooth the data and reduce the variability.

This procedure results in a time course of band power values, including phase-locked and not phase-locked power changes as well. For the discrimination of both types of power changes, the procedure described above should be complemented with another one where the step of squaring the filtered amplitudes is omitted, as follows:

1. bandpass filtering;
2. calculation of the point-to-point intertrial variance;
3. averaging over time.

The difference between both ERD/ERS calculating procedures is described by Kalcher and Pfurtscheller (1995). It was found that in the case of lower frequency components (lower alpha and theta bands), a phase-locked power increase due to the ERP can mask the non-phase-locked power decrease (ERD) when the 'classical' band-power method is used. The different methods used today for ERD/ERS quantification are summarized in Table 1.

To obtain percentage values for ERD/ERS, the power within the frequency band of interest in the period after the event is given by A whereas that of the preceding baseline or reference period is given by R. ERD or ERS is defined as the percentage of power decrease or increase, respectively, according to the expression $ERD\% = (A - R)/R \times 100$.[1] For the display of the time course of

ERD/ERS, a scale displaying either power changes with 0% in the reference period or relative power with 100% in the reference period is recommended. The total procedure of ERD/ERS calculation is displayed in Fig. 3 with one example of dominant ERD in the alpha band on the left side and one example with dominant ERS in the beta band on the right side. Further details can be found elsewhere (Pfurtscheller et al., 1999).

3.2. Spatial mapping of ERD/ERS

Multichannel EEG signals are usually recorded against a common reference electrode. The data are therefore reference-dependent. To convert the reference-dependent raw data in reference-free data, different methods are available and discussed in detail by Lopes da Silva et al. (1993); Pfurtscheller (1992); Pfurtscheller et al. (1994b) : (i) Common average reference (ii) Laplacian reference (iii) Local average reference. Reference-free maps (e.g. surface Laplacian) generally show a more focal pattern as compared to referential maps and are especially recommended when data corresponding to a movement task are analyzed.

For spatial mapping of ERD/ERS, different methods are available as, for example, the calculation of surface Laplacian, cortical imaging and distributed source imaging. References to different deblurring methods, either using a realistic head model or a spherical model, are summarized
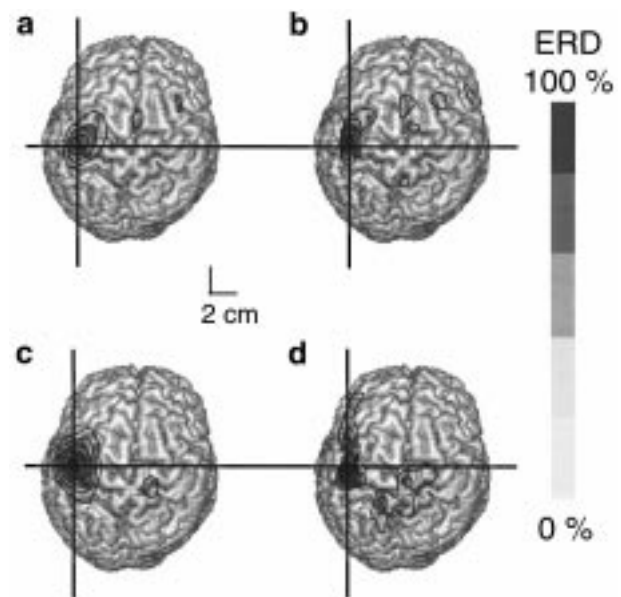

Fig. 4. ERD distributions calculated prior to a right hand movement. Maps are viewed from above. (a) Spline surface Laplacian calculated on a realistic head model. (b) Spline surface Laplacian calculated on a spherical head model and displayed over a realistic head model. Note the focus of ERD over the cortical representation area of the left hemisphere. (c) Linear estimation results based on a realistic head model. (d) Linear estimation results based on a spherical head model and displayed on the realistic head model. The maximum ERD value in (d) is found 0.5 cm posterior compared to (c). The ERD is scaled to its maximal value for each method, (modified from van Burik et al., 1999).

[1] In earlier publications the following definition was used: $ERD\% = (R - A)/R \times 100$. With this definition, negative numbers are obtained for ERS%. Because ERD is defined as power decrease and ERS as power increase it is more precise when the following expression is used: $ERD\% = (A - R)/R \times 100$.
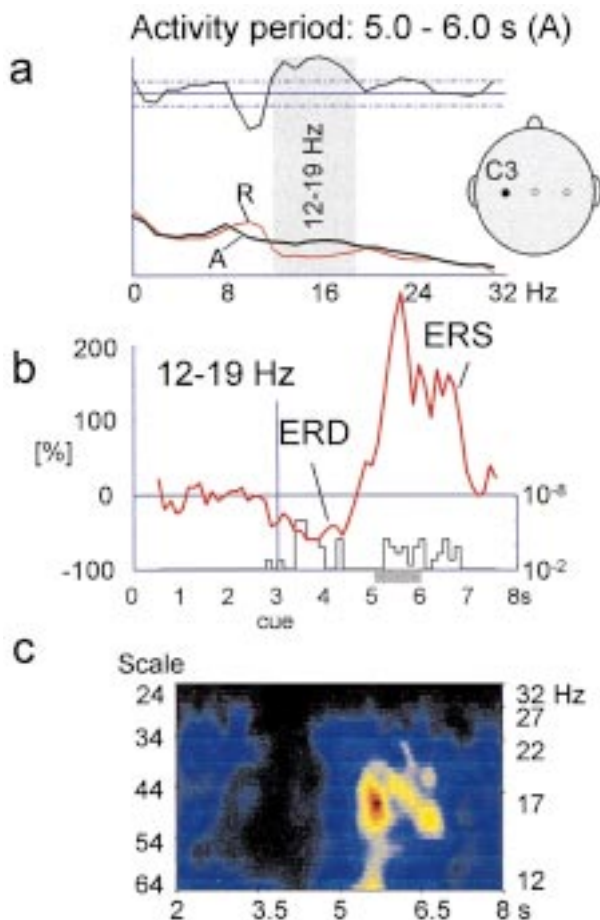
Fig. 5. (a) Superimposed logarithmic 1-s power spectra calculated in the reference period (R) and the activity period (A) during cue-triggered finger movement as well as the difference between the two spectra with 95% confidence intervals indicated by the dotted lines. The frequency range displaying significant power increase is marked. (b) Band power time course calculated for the frequency band indicated in (a) triggered according to cue-onset (vertical line) and significance level (sign test P from 10^{-2} to 10^{-8}) for power changes (step function). A power decrease indicates ERD and a power increase ERS. The horizontal line marks the band power in the reference period. (c) Scalogram displaying the squared and over all trials averaged wavelet coefficients for the time interval 2 to 8 s (x-axis). Scale (left axis) running from 24 to 64 corresponds to a frequency range (right axis) from 12 to 32 Hz. Color-scale from 'black' (minimum) to 'red' (maximum): The maximum is marked by a cross.

in Table 2. For a detailed description see van Burik and Pfurtscheller (1999); van Burik et al. (1999).

An example of ERD maps calculated with spline surface Laplacian and Linear Estimation prior to right hand movement is displayed in Fig. 4. For the calculation, a realistic head model (a,c) and a spherical head model (b,d) were used. As can be seen there are only marginal differences in the location of the ERD focus with these different methods.

4. Determination of subject-specific frequency bands

One of the most important questions in ERD/ERS analy-

sis is how to determine the upper and the lower limits of the bandpass filter. The following methods can be used:

1. detection of the most reactive frequency band based on the comparison of two short-term power spectra;
2. continuous wavelet transform (CWT);
3. definition of frequency bands relative to the spectral peak frequency.

4.1. Comparison of short-time power spectra

The first method is based on the comparison of two 1-s power spectra calculated over a number of event-related EEG trials. One spectrum is calculated for the reference period (R) chosen some seconds before an event occurs, and the other is calculated for the activity period (A). In a movement task this active period can be chosen as a period during the planning phase before movement-onset, during movement execution or during the recovery phase after movement-offset. The difference curve between the 2 logarithmic power spectra of periods A and R, together with the 95% confidence interval, can be used to determine the significant frequency components, which either display a power increase (ERS) or power decrease (ERD) in the active period as compared to the reference period.

An example from a cue-paced right finger movement experiment is given in Fig. 5. The two 1-s power spectra shown are calculated in the reference period (thin line) and in the activity period 5.0–6.0 s (thick line, Fig. 5a). The difference curve of the two logarithmic spectra show one interval with a significant power increase. A gray bar highlights the corresponding frequency band. The ERD time course calculated for the subject-specific frequency band is displayed in Fig. 5b. The step function, superimposed under the ERD curve, indicates the significance of band power changes in 125-ms intervals (sign-test, details see Pfurtscheller, 1992). The most significant ERS was found in the 12–19 Hz band. This example demonstrates quite well the importance of selecting subject-specific frequency bands.

4.2. Continuous Wavelet Transform (CWT)

The CWT compares a signal with dilated and shifted versions of a basic wavelet ψ according to the following integral (Chui, 1994):

$$\left(W_\psi f \right)(b, a) = \int_{-\infty}^{+\infty} f(t)\psi^*_{b,a}(t)dt.$$

The amount of dilation of the wavelet ψ is represented by the scale a and the shifting of the wavelet by parameter b:

$$\psi_{b,a}(t) = |a|^{-1/2}\psi\left(\frac{t-b}{a}\right).$$

The unique characteristics of the CWT are revealed by the time and frequency resolution of the transform at a specific scale a. When ω_o is the center frequency of the

basic wavelet's spectrum, then the center frequency of the dilated wavelet at scale a will be ω_o/a. Applying the CWT at scale a, local spectral information is obtained of the signals at frequency ω_o/a with a time resolution of $2\Delta_{\hat{\psi}}/a$ whereby Δ_{ψ} is the radius of the wavelet (root mean square duration) and $\Delta_{\hat{\psi}}$ the RMS bandwidth. This is what makes the CWT so suitable for EEG analysis: high frequencies (low scale) are analyzed with a high time resolution and a low frequency resolution, whereas low frequencies (high scale) are analyzed with a low time resolution and a high frequency resolution (Pasterkamp, Technical Report, University of Twente, Feb. 1999).

Wavelet transformation was also applied to the same data as used in Fig. 5a. The scalogram for scale $a = 24$ to $a = 64$ and the time window 2–8 s is shown in Fig. 5c. The peak found at 16.5 Hz marks the maximum of the beta rebound (beta ERS) at second 5.7. The peak frequency of the beta ERS at 16.5 Hz is much more accurate than when found with the spectral method as shown in Fig. 5a.

4.3. Determination of frequency bands dependent on the peak frequency

Due to large inter-individual differences of the alpha frequency, large portions of alpha band power may fall outside a fixed frequency window eventually resulting in misleading interpretations. In order to avoid these and related problems arising with fixed frequency windows, the group of Klimesch (Klimesch et al., 1998; Doppelmayr et al., 1998) suggests the use of a mean alpha peak center of gravity (centroid) frequency $f(i)$ as an anchor point to adjust frequency bands individually. Four frequency bands with a width of 2 Hz can be defined in relation to $f(i)$ that cover the traditional theta and alpha frequency range from about 4–12 Hz (depending on the actual $f(i)$ of each subject). The frequency bands obtained by this method are termed by Klimesch's group as: theta ($f(i) - 6$ to $f(i) - 4$); lower 1 alpha ($f(i) - 4$ to $f(i) - 2$); lower 2 alpha ($f(i) - 2$ to $f(i)$) and upper alpha ($f(i)$ to $f(i) + 2$). ERD is calculated within these individually determined frequency bands. In contrast to the group of Klimesch we recommend that the frequency bands should always be given explicitly in Hz and not by using the term 'alpha', particularly in those cases where the bands of interest lie outside, or overlap, the limits of the well-defined and classic frequency bands.

5. ERD in memory and movement tasks

The alpha band rhythms demonstrate a relatively widespread desynchronization (ERD) in perceptual, judgement and memory tasks (Van Winsum et al., 1984; Sergeant et al., 1987; Pfurtscheller and Klimesch, 1992; Klimesch et al., 1992, 1993, 1994; Aftanas et al., 1996; Sterman et al., 1996). An increase of task complexity or attention results in an increased magnitude of ERD (Boiten et al., 1992; Dujardin et al., 1993). It has to be kept in mind, however,

that the ERD is measured in percentage of power relative to the reference interval and therefore it depends on the amount of rhythmic activity in this interval.

It is important to note that alpha band desynchronization is not a unitary phenomenon. If different frequency bands within the range of the extended alpha band are distinguished, at least two distinct patterns of alpha desynchronization can be observed. Lower alpha desynchronization (in the range of about 7–10 Hz) is obtained in response to almost any type of task. It is topographically widespread over wide areas of the scalp and probably reflects general task demands and attentional processes. Upper alpha (mu) desynchronization (in the range of about 10–12 Hz) is very often topographically restricted and develops during the processing of sensory-semantic information above parieto-occipital areas (Klimesch et al., 1993, 1994, 1996a, 1997). The degree of desynchronization is closely linked to semantic memory processes. For example, during semantic encoding of words, good memory performers showed a significantly larger ERD in the lower alpha band as compared to bad performers (Klimesch et al., 1996a; Sterman et al., 1996). An explanation for this finding may be that a higher level of attention and alertness is required during encoding. In contrast to the alpha band activities, the activity in the theta band may be responsible for the encoding of new information (Klimesch et al., 1996b; Klimesch, 1999).

In an auditory memory task, no localized alpha band ERD was found in ongoing EEG (Krause et al., 1996; Karrasch et al., 1998). This absence of an alpha band desynchronization in EEG during the memory set presentation may be explained by the anatomical localization of the auditory cortex in the supratemporal plane. EEG desynchronization due to direct auditory processing alone is, therefore, hard to detect in scalp-recorded EEG. On the contrary, a desynchronization localized to the auditory cortex following auditory stimuli was reported in MEG recordings (Tiihonen et al., 1991).

Voluntary movement results in a circumscribed desynchronization in the upper alpha and lower beta bands, localized close to sensorimotor areas (Pfurtscheller and Aranibar, 1979; Pfurtscheller and Berghold, 1989; Derambure et al., 1993; Toro et al., 1994; Stancák and Pfurtscheller, 1996b; Leocani et al., 1997). This desynchronization starts about 2 s prior to movement-onset over the contralateral Rolandic region and becomes bilaterally symmetrical immediately before execution of movement. It is of interest that the time course of the contralateral mu desynchronization is almost identical with brisk and slow finger movement, although both, brisk and slow movements are quite different. Brisk movement is preprogrammed and it does not require feedback from the periphery, while slow movement depends on the reafferent input from kinesthetic receptors evoked by the movement itself (Stancák and Pfurtscheller, 1996a). Analysis of alpha and beta ERD using electrocorticographic (ECoG) recordings showed that the topography of
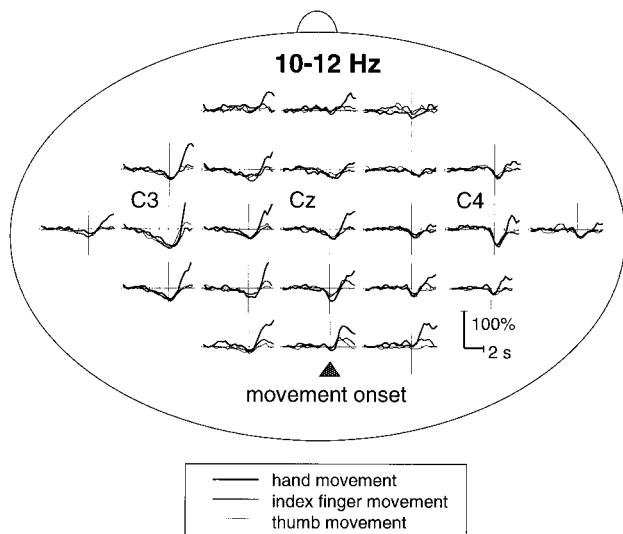
Fig. 6. Topographic display of grand average ERD curves from three movement experiments. Data are triggered with movement-onset (vertical line). The reference interval (base line) is marked by a horizontal line. (Modified from Pfurtscheller et al., 1999).

beta ERD was often more discrete and somatotopically specific than that of alpha ERD (Crone et al., 1998a).

The contralateral dominant pre-movement mu ERD is not only independent of movement duration, but also similar with index finger, thumb and hand movement. An example of a group data study (Pfurtscheller et al., 1998a) is given in Fig. 6. One interpretation of these findings is that the contralateral pre-movement mu desynchronization reflects a relatively unspecific pre-activation, priming or presetting of neurons in motor areas which is not only fairly independent of the speed (e.g. brisk vs. slow) but also of the type of forthcoming movement (e.g. wrist vs. finger).
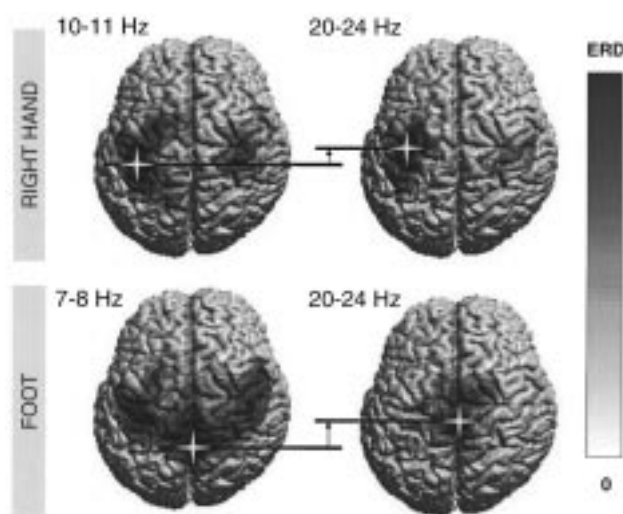

Fig. 7. ERD maps on a realistic head model from one subject during voluntary right hand (upper panel) and voluntary foot movement (lower panel). Data are displayed for subject-specific frequency bands showing largest power decrease. The maps represent a time interval of 125 ms. The white cross marks the maximum ERD.

While a circumscribed hand area mu ERD can be found in nearly every subject (Pfurtscheller and Aranibar, 1979; Pfurtscheller and Berghold, 1989), a foot area mu ERD localized close to the primary foot area between both hemispheres is less frequent (Pfurtscheller et al., 1997a). An example of a relatively widespread foot area desynchronization in the 7–8 Hz band and a circumscribed 20–24 Hz band ERD is presented in Fig. 7. For comparison, also a hand area mu desynchronization in the 10–11 Hz band, with a beta desynchronization in the 20–24 Hz band, is displayed. It is of interest that the localization of the beta ERD is slightly more anterior compared to the largest mu ERD with hand as well as the foot movement and that the 7–8 Hz-ERD with foot movement is found not only over the foot but also over the hand representation area. This can be interpreted as follows: the mu rhythm is generated mainly in the post-Rolandic somatosensory area and the central beta rhythm (at least some components of it) in the pre-Rolandic motor area. An investigation of hand area mu and beta rhythms on single trial basis also revealed a slightly more anterior focus of the beta rhythm (Pfurtscheller et al., 1994). MEG measurements made by Salmelin et al. (1995) revealed a similar result. They interpreted the 10-Hz mu rhythm as localized in the primary somatosensory area and the 20-Hz beta rhythm as localized in the motor area.

In an electrophysiological study with subdural electrodes, Arroyo et al. (1993) reported on mu rhythms not only selectively blocked with arm and leg movements, but also with face movement. It can therefore be hypothesized that beside a great variety of occipital alpha rhythms (Grey Walter in Mulholland et al. (1969)) also a variety of Rolandic mu rhythms exist.

6. Simultaneous occurrence of ERD and ERS in the alpha and lower beta bands

A visual input results not only in a desynchronization of occipital alpha rhythms but also in an enhancement or synchronization of central mu rhythms. Brechet and Lecasble (1965) reported on an enhanced mu rhythm during flicker stimulation, Koshino and Niedermeyer (1975) on enhanced (synchronized) Rolandic rhythms during pattern vision and Pfurtscheller (1992) on a central alpha power increase in a reading task. The opposite, an enhancement of occipital alpha rhythms and desynchronization of central mu rhythms, is found, e.g. during self-paced, voluntary hand movement (Pfurtscheller, 1992).

An example from a group study on nine normal subjects performing self-paced hand movement demonstrates a contralateral localized mu rhythm ERD and an occipital localized alpha rhythm ERS (Fig. 8a). It is of interest to note that after termination of the movement the central region exhibits a localized ERS (for details see Section 7).

Such an antagonistic behavior can occur not only between two different modalities but also within the same modality.
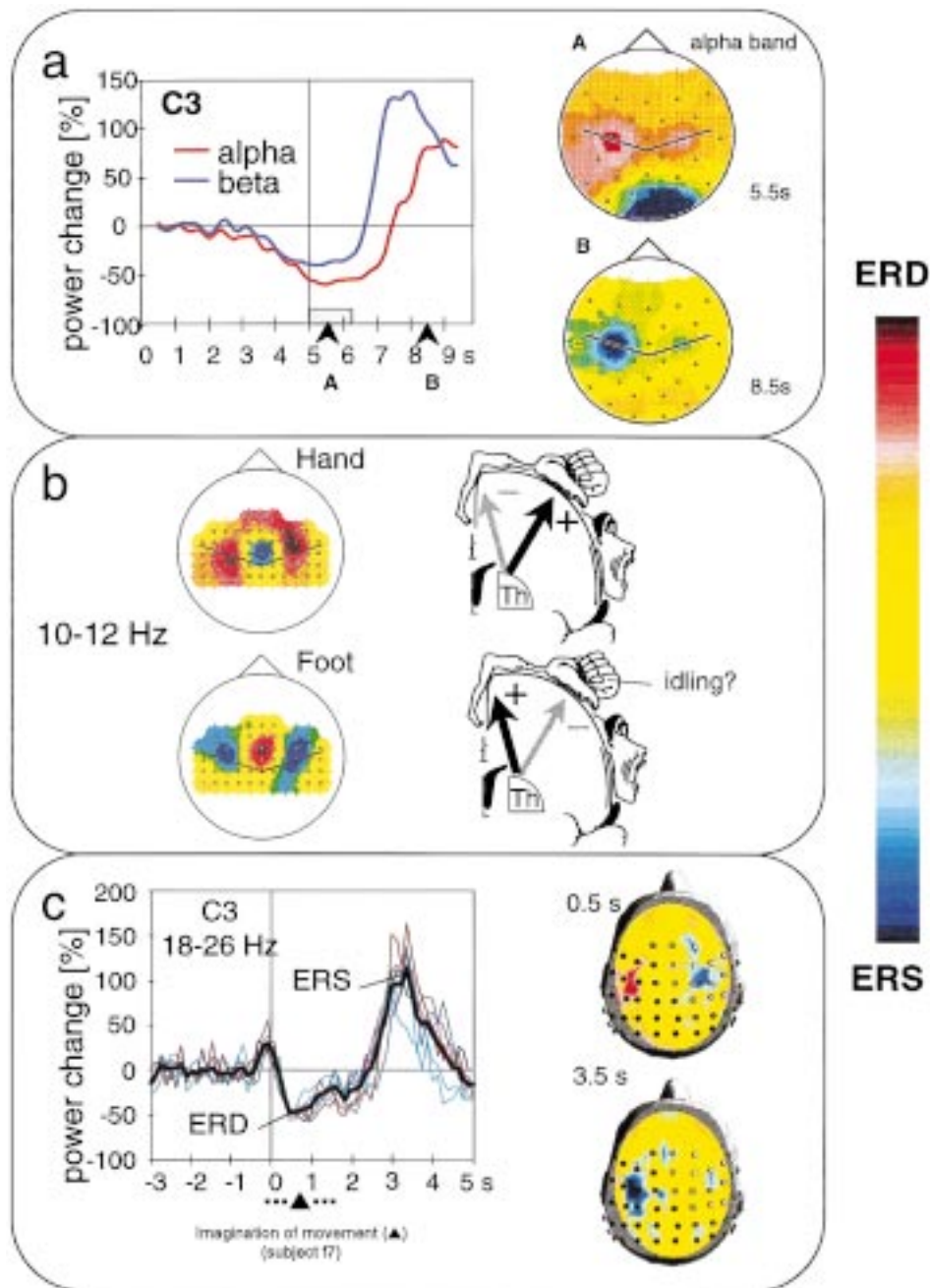
Fig. 8. (a) Grand average ($n = 9$) ERD curves calculated in the alpha and beta bands in a right hand movement task (left side). Grand average maps calculated for a 125 ms interval during movement (A) and after movement-offset in the recovery period (B) (right side). (b) Maps displaying ERD and ERS for an interval of 125 ms during voluntary movement of the hand (left, upper panel) and movement of the foot (left, lower panel). The motor homunculus with a possible mechanism of cortical activation/deactivation gated by thalamic structures is shown on the right. (c) Superimposed ERD curves with beta rebound from eight sessions with right motor imagery in one subject. Analyzed frequency band 18–26 Hz, EEG recorded from electrode position C3. In addition to the individual curves also the grand average ERD curve is plotted (left side). ERD maps from one session displaying simultaneous contralateral ERD and ipsilateral ERS during and contralateral ERS after motor imagery (right side). The scalp electrode positions are marked, (modified from Pfurtscheller et al., 1997c). 'Red' indicates power decrease or ERD and 'blue' power increase or ERS.

For example voluntary hand movement can result in a hand area ERD and simultaneously in a foot area ERS, and voluntary foot movement can result in an opposite pattern as shown in Fig. 8b (Pfurtscheller and Neuper, 1994; Pfurtscheller et al., 1997a). Common for the enhanced hand area mu rhythm during visual information processing and during foot movement is that in both cases the hand area is not directly involved in the task and therefore the hand area network may be in a deactivated state.

A possible explanation of the antagonistic behavior of ERD and ERS in the alpha and lower beta band is depicted in Fig. 8b, right side. Thalamic structures (interplay between
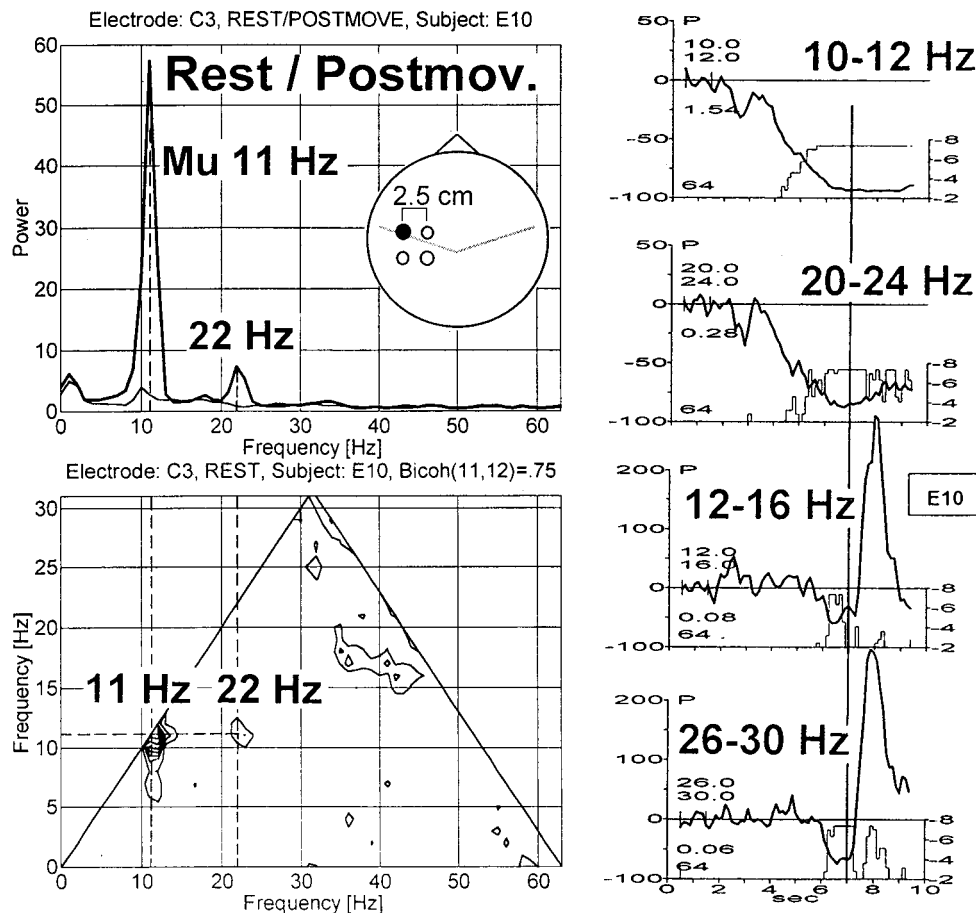
Fig. 9. Examples of 1-s power spectra calculated from EEG data (electrode C3) recorded during rest (thick line) and during movement (thin line; left upper panel). The reference spectrum shows two peaks at 11 and 22 Hz which are attenuated with movement. The bicoherence displays a quadratic phase coupling between 11 and 22 Hz with a maximal coherence of 0.79 (left lower panel).Time evolution of band power changes calculated in the indicated frequency bands (right side). Brisk movement-offset is marked with a vertical line at second 7. In addition to the power changes (thick line), the significance levels of power changes (thin line) are indicated. The scale on the right indicates significance levels 10^{-2} to 10^{-8} (sign test); the scale on the left gives percentage power changes (modified from Pfurtscheller et al., 1997b).

thalamic relay nuclei and cells of the thalamic reticular nucleus) activate such cortical areas involved at a certain moment of time for processing of relevant information and deactivate at the same time other cortical areas that are not used to perform the task. A simulation study supporting this model of 'focal ERD/surround ERS' is reported by Suffczynski et al. (1999).

Another example of the simultaneous occurrence of ERD and ERS in the beta band is presented in Fig. 8c. Imagery of right hand movement can be accompanied by a contralateral beta ERD and an ipsilateral beta ERS. Both patterns are circumscribed and localized close to the hand areas (Pfurtscheller and Neuper, 1997).

7. Post-movement beta ERS

One interesting oscillating brain signal, with a relatively good signal-to-noise ratio in the human scalp EEG, is the post-movement beta ERS. These induced beta oscillations are found in the first second after termination of a voluntary movement, when the Rolandic mu rhythm still displays a desynchronized pattern of low amplitude. This low amplitude activity, with a focus around the corresponding sensorimotor representation area, results in embedded beta oscillations with a good signal-to-noise ratio. Examples of post-movement beta oscillations from different subjects with frequencies around 14, 19 and 23 Hz are displayed elsewhere (Pfurtscheller et al., 1997b; Fig. 3 and Fig. 5).

Special care has to be taken regarding the identification of reactive beta bands. The reason for this is that the Rolandic mu rhythm, which is very often arch-shaped (Gastaut, 1952), presents in most cases 2 peaks in the power spectrum - one in the alpha and the other in the beta frequency ranges (Fig. 9, left side). In such cases it is not simple to conclude that two independent rhythms are present. Whether or not the two spectral peaks are harmonically related can be tested by computing the bicoherence (Kim and Powers, 1979). An
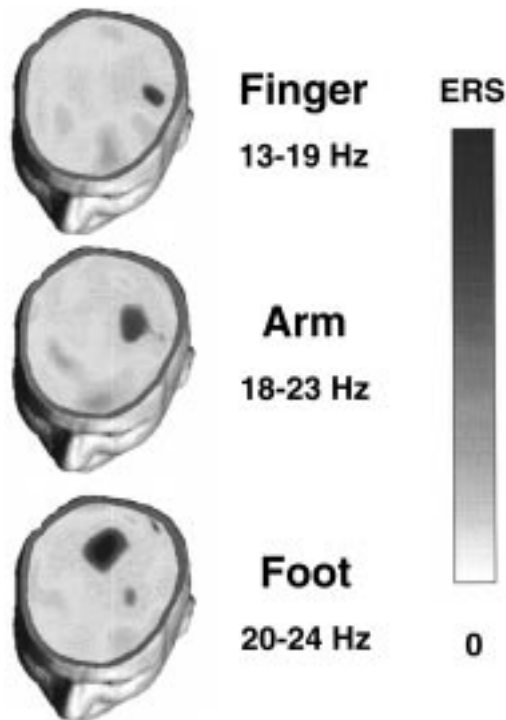
Fig. 10. Movement-specific location of the beta ERS in one subject displaying a somatotopic organization of the beta oscillations after finger, arm and foot movement. Note the different subject-specific frequency bands lowest with finger and highest with arm and foot movement, respectively. 'Black' indicates location of maximal ERS.

example for such a power spectrum with peaks at 11 and 22 Hz and the corresponding bicoherence plots is shown in Fig. 9. The interpretation of the bicoherence plot is that 79% (BICOH = 0.79) of the power at 22 Hz can be explained by non-linear coupling with the 11-Hz wave. Power time courses for the frequency bands 10–12, 20–24, 12–16 and 26–30 Hz are displayed on Fig. 9, right side. The non-linear coupling of the 11- and 22-Hz oscillations is documented by the similar ERD curves in the 10–12 and 20–24 Hz frequency bands. A different behavior, on the other hand, is found in the beta bands of 12–16 and 26–30 Hz. These two frequency bands also display harmonic frequency components and are non-linearly coupled (Pfurtscheller et al., 1997b).

The post-movement beta ERS (Pfurtscheller et al., 1996) displays the following features:

1. the beta ERS has a somatotopic organization (Salmelin et al., 1995; Neuper and Pfurtscheller, 1996);
2. the beta ERS is significantly larger with hand as compared to finger movement (Pfurtscheller et al., 1998a);
3. the beta ERS is found not only after a really executed but also after an imagined movement (Neuper and Pfurtscheller, 1999);
4. the maximum of the beta ERS coincides with a reduced excitability of motor cortex neurons (Chen et al., 1998).

The post-movement beta ERS is a relatively robust phenomenon and is found in nearly every subject after finger, hand, arm and foot movement (Pfurtscheller et al., 1998a; Pfurtscheller et al., 1999). It is dominant over the contralateral primary sensorimotor area and has a maximum around 1000 ms after movement-offset. The beta bursts can include frequency components either in a single band or in multiple frequency bands, whereby each person has his own subject-specific beta frequency components. For finger movement the largest beta ERS was found in the 16–21 Hz band, (Pfurtscheller et al., 1997b) and for foot movement in the slightly higher 19–26 Hz band (Neuper and Pfurtscheller, 1996).

An example for the somatotopic organization of the post-movement beta ERS with finger, arm and foot movement is given in Fig. 10. This corresponds to the findings of Salmelin et al. (1995) on the rebound of the 20-Hz rhythms in MEG following finger, toe and mouth movement. They reported on a motorotopic organization of the beta bursts and emphasized its sources in the anterior wall of the central sulcus.

Band power time courses displaying post-movement beta ERS after brisk and slow finger movement experiments were reported by Stancák and Pfurtscheller (1997). Although both types of movement are quite different – the former is preprogrammed and the latter feedback-controlled – the patterns of the post-movement beta ERS differ only slightly, with a greater rebound in the time interval 0.25–0.75 s relative to movement-offset after brisk than after slow movement. This can be interpreted as the enhanced beta oscillations after termination of movement depend less on cutaneous and proprioceptive afferences and more on the preceding activation of the motor area. A shift of the motor cortex neurons from an activated state to a deactivated state may condition the occurrence of beta oscillations (Pfurtscheller et al., 1996). Support for this hypothesis comes from imagination experiments without EMG activity (Pfurtscheller et al., 1997c) where in some subject also a post-imagination beta ERS could be observed. This type of beta ERS is also very stable and was found in different sessions with the same subject (Fig. 8c, left side). In addition to the superimposed band power curves for eight sessions, the topographical localization from one session is displayed in Fig. 8c on the right. As can be seen, the beta ERS after imagination shows a similar location over the contralateral hand representation area as compared to the post-movement beta ERS. A similar somatotopic mapping of the primary motor cortex in humans was found in activation studies with cerebral blood flow measurements (Grafton et al., 1991).

In order to control finger movement a large number of muscle spindles involved, whereas for the movement of the wrist, muscle force is required and hence more mass of muscular fibers has to be activated. Finger movement is accompanied by both cutaneous and proprioceptive afferences, whereas wrist movement results in more propriocep-

tive activity from the joints. For the activation of a larger muscle mass, a relatively larger population of cortical neurons is required. The finding of larger amplitude beta oscillations with wrist as compared to finger movement can be interpreted as the change of a larger population of motor cortex neurons from an increased neural discharge (activation) during the motor act to a state of cortical disfacilitation or deactivation after movement-offset.

Considering that, for example, each finger cortical area has its own specific beta generating network, the simultaneous movement of two or more fingers is expected to result in a larger beta ERS than the movement of only one finger (Pfurtscheller et al., 1999). The large beta ERS after wrist movement may therefore be explained as the result of a cumulative effect over a larger population of neuronal assemblies.

Of great importance for the interpretation of the post-movement beta ERS is the work of Chen et al. (1998) on transcranial magnetic stimulation of the motor cortex and corticospinal excitability. This corticospinal excitability was increased during thumb movement and decreased from 500 to 1000 ms after EMG offset. The period of decreased corticospinal excitability after movement corresponds to the occurrence of the post-movement beta ERS and supports the hypothesis that the beta ERS may be related to a deactivated state of the motor cortex.

8. Interpretation of ERD and ERS in the alpha and lower beta band

Increased cellular excitability in thalamo-cortical systems results in a low amplitude desynchronized EEG (Steriade and Llinas, 1988). Therefore, ERD can be interpreted as an electrophysiological correlate of activated cortical areas involved in processing of sensory or cognitive information or production of motor behavior (Pfurtscheller, 1992). An increased and/or more widespread ERD could be the result of the involvement of a larger neural network or more cell assemblies in information processing. Factors contributing to such an enhancement of the ERD are increased task complexity, more efficient task performance (Sterman et al., 1996; Dujardin et al., 1993; Klimesch et al., 1996a; Boiten et al., 1992) and/or more effort and attention as needed in patients, elderly or lower IQ subjects (Defebvre et al., 1996; Derambure et al., 1993; Neubauer et al., 1995; Neubauer et al., 1999).

Explicit learning of a movement sequence, e.g. key pressing with different fingers, is accompanied by an enhancement of the mu ERD over the contralateral central regions. Once the movement sequence has been learned and the movement is performed more 'automatically', the ERD is reduced. These ERD findings strongly suggest that activity in primary sensorimotor areas increases in association with learning a new motor task and decreases after the task has been learned (Zhuang et al., 1997). The involvement of the

primary motor area in learning motor sequences was also suggested by Pascual-Leone et al. (1995) who studied motor output maps by transcranial magnetic stimulation.

The opposite phenomenon to ERD is an increase in a spectral peak at a given frequency component that we call event-related synchronization or ERS. In this case the amplitude enhancement is based on the cooperative or synchronized behavior of a large number of neurons (Pfurtscheller et al., 1996b). When the summed synaptic events become sufficiently large, the field potentials can be recorded not only with macro electrodes within the cortex, but also with surface electrodes over the scalp. Large alpha or mu waves in the EEG/MEG need coherent activity of cell assemblies over at least several square centimeters (Cooper et al., 1965; Lopes da Silva, 1991). When patches of neurons display coherent activity in the alpha band, an active processing of information is very unlikely and it may be assumed that the corresponding networks are in a deactivated state.

It is of interest to note that about 85% of cortical neurons are excitatory, with the other 15% being inhibitory (Braitenberg and Schüz, 1991). Inhibition in neural networks is, however, very important, not only to optimize energy demands but also to limit and control excitatory processes. Klimesch (1996) suggested that synchronized alpha band rhythms during mental inactivity (idling) may be important to introduce powerful inhibitory effects, which could act to block a memory search from entering irrelevant parts of neural networks.

Adrian and Matthews (1934) described a system which is neither receiving nor processing sensory information as an 'idling system'. Localized synchronization of 12–14 Hz components in awake cats was interpreted by Chase and Harper (1971) as a result of 'idling cortical areas'. Cortical idling can thus denote a cortical area of at least some cm^2 which is not involved in processing sensory input or preparing motor output. In this sense, occipital alpha rhythms can be considered as 'idling rhythms' of the visual areas and mu rhythms as 'idling rhythms' of sensorimotor areas (Kuhlman, 1978).

Bursts of synchronized sensorimotor rhythms (SMR) are not only seen in cats during alert motionless waking behavior, but also in quiet sleep (Sterman et al., 1970; Howe and Sterman, 1972). Sleep spindles during the early sleep stages are apparently correlated with a block of synaptic transmission through the thalamus (Steriade and Llinas, 1988).

It has to be mentioned, however, that there are also reports on induced (synchronized) alpha band rhythms before omitted stimuli (Basar et al., 1989). This short-term alpha enhancement is found when a subject expected a defined sensory stimulus. Also, Klimesch et al. (1992) reported an increase of power in the lower alpha band prior to the imperative stimulus in a category judgement task. These findings are not in contradiction to the –idling hypothesis–, where it is assumed that there are always, at the same instant time, activated and deactivated cortical areas

Right Finger Movement
slow   brisk

mu ERD

mu
~6μV

0.5 s

beta ERS
(idling ?)

central
beta
~1.5μV

%
200

100

40-Hz ERS
(processing)

40 Hz
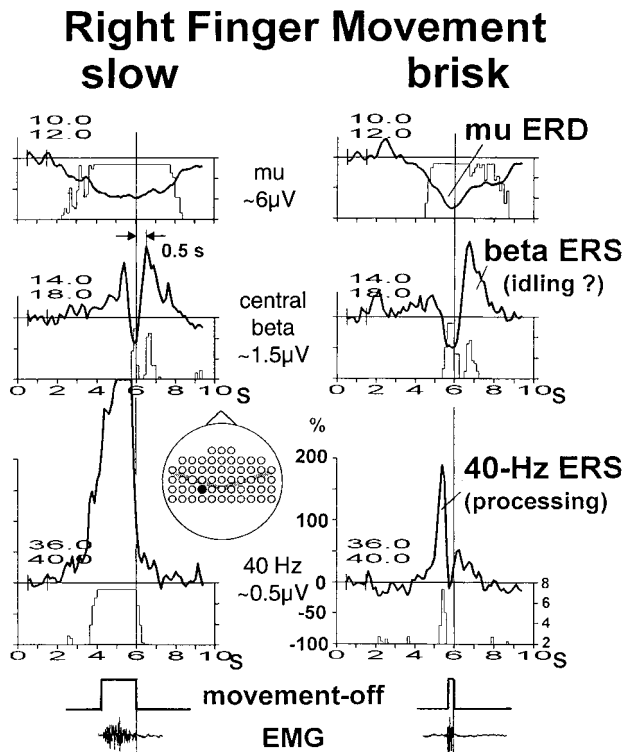~0.5μV

0
-50
-100

movement-off

EMG

Fig. 11. ERD/ERS time courses from one subject computed during self-paced voluntary slow (left side) and brisk finger movement (right side). Data of three frequency bands (10–12, 14–18 and 36–40 Hz) are displayed. The data are triggered with respect to movement-offset (vertical line at second 6). Note the different time courses and duration of mu ERD, beta ERS and gamma ERS. The approximate amplitudes (square root of band powers) for the mu, beta and gamma bands are 6, 1.5 and 0.5 μV, respectively.

during performance of a specific task. Or in other words, there are always scalp electrodes showing synchronized and desynchronized alpha (beta) band rhythms at the same moment of time (Pfurtscheller, 1992; Westphal et al., 1993; Hughes et al., 1995 and examples in Fig. 8).

9. ERS in the gamma band

In addition to oscillations in the alpha and lower beta bands, induced oscillations are also found in the frequency band around 40 Hz. Such oscillations were reported with visual stimulation (Gray et al., 1988) and in a movement task (Murthy and Fetz, 1992; Rougeul et al., 1979; Pfurtscheller et al., 1993) and may be related to a binding of sensory information and sensorimotor integration, respectively. Oscillations in the alpha and lower beta range would be too slow to serve as carrier signals for binding at a higher level of processing. However, oscillations in the gamma band appear appropriate to establish rapid coupling or synchronizing between spatially separated cell assemblies (Singer, 1993).

The existence of at least three different types of oscilla-

tions at the same electrode location over the contralateral sensorimotor hand area during brisk and slow finger lifting is documented in Fig. 11. Beside a mu desynchronization (10–12 Hz) and a post-movement beta synchronization (14–18 Hz), induced gamma oscillations (36–40 Hz) are also present. These 40-Hz oscillations reveal their maximum shortly before movement-onset and during execution of movement, respectively, whereas the beta ERS has its maximum after movement-offset. Of interest are the different amplitudes of mu, central beta and gamma oscillations with the greatest amplitude (square root of power) with mu and the smallest with gamma activity. Further details on movement-related gamma oscillations in man are found elsewhere (Pfurtscheller et al., 1993; Salenius et al., 1996).

In contrast to the alpha band rhythms, the gamma oscillations reflect a stage of active information processing. A prerequisite for the development of gamma bursts may be the desynchronization of alpha band rhythms. The example in Fig. 11 shows that induced gamma and beta oscillations are embedded in desynchronized alpha band activity with brisk as well as slow movement. In this context it is interesting to note that recently Crone et al. (1998b) found that when using electrocorticographic (ECoG) recordings, the cortical topography of gamma ERS is more consistent with the functional anatomy of sensorimotor cortical maps than alpha or beta ERD.

Separate foci of synchronized gamma activities occurring in cortical regions which are widely separated–often even in different lobes–can display high correlation during the performance of cognitive or motor tasks. Bressler et al. (1993) reported on task-related increases in high-frequency coherence in the monkey neocortex during the performance of a pattern-discrimination task; gamma band activities in the striate and motor cortex were briefly correlated when a motor response occurred and were uncorrelated when no response occurred. Andrew and Pfurtscheller (1996) reported a phasic increase of coherence of 40-Hz oscillations between the contralateral sensorimotor and the supple-
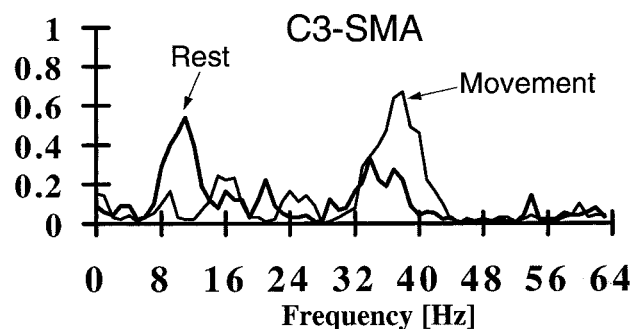
C3-SMA

Rest

Movement

Frequency [Hz]

Fig. 12. Coherence function (squared coherence) calculated from 1-s epochs in the reference interval prior to voluntary right hand movement (thick line) and during movement (thin line). Data recorded over left hand area (electrode position C3) and over midfrontal areas (electrode position about 5 cm anterior to Cz).

mentary motor areas during the performance of unilateral finger movements. In contrast, no changes in 40-Hz coherence were found between the left and right sensorimotor areas during the movement. These findings suggest that an increase in gamma band coherence is functionally related to the performed task. Fig. 12 shows two coherence functions calculated between primary sensorimotor and supplementary motor areas, one calculated in the reference period some seconds before initialization of a self-paced finger movement and the other during movement execution. In the reference period (resting condition), there is a linear coupling of rhythms in the alpha band between both areas whereas during movement a linear coupling is found in the gamma band. Whether changes in coherence always reflect changes in functional coupling is, however questionable (Florian et al., 1998).

10. ERD/ERS in neurological disorders

The quantification of movement-related desynchronization can improve the diagnosis of functional deficits in patients with cerebrovascular disorders and Parkinson's disease (PD). It was shown that there is a high correlation between morphological and functional findings in cerebrovascular disorders. The ERD is reduced or abolished over the affected hemisphere. Based on ERD measurements during voluntary hand movement it was, for example, possible to differentiate between superficial and deep vascular lesions (Pfurtscheller et al., 1981). In case of PD, the premovement ERD is less lateralized over the contralateral sensorimotor area and starts later than in control subjects (Defebvre et al., 1993; Defebvre et al., 1994; Defebvre et al., 1996; Defebvre et al., 1998; Magnani et al. 1998). Beside the ERD, the post-movement beta ERS is also affected in PD when a subject executes a self-paced movement with one hand (Diez et al., 1999; Pfurtscheller et al., 1998b). The beta ERS is of smaller magnitude and it is delayed as compared to controls. Assuming that the beta ERS is a measure of recovery of the primary motor area after movement, the reduced beta ERS should indicate its impaired recovery in PD patients. ERD changes in epilepsy with focal motor seizures were reported by Derambure et al. (1997). For further details seePfurtscheller and Lopes da Silva (1999), Chapters 24–27.

Acknowledgements

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