Epilepsia, **44**(Suppl. 12):2–8, 2003
Blackwell Publishing, Inc.

Induced Oscillations in the Alpha Band: Functional Meaning

G. Pfurtscheller

Department of Medical Informatics, Institute of Biomedical Engineering and Ludwig Boltzmann Institute for Medical Informatics and Neuroinformatics, Technical University Graz, Graz, Switzerland

Summary: The phenomena of event-related desynchronization (ERD) and synchronization (ERS) reflect the dynamics of neural networks and can be observed on different scalp locations at the same moment of time. Whereas on one cortical area a focal 10-Hz ERD can be found, other areas can display a 10-Hz ERS. This phenomenon is called *focal ERD/surround ERS* and is interpreted as a correlate of an activated cortical area (ERD) and simultaneously deactivated or inhibited other areas. The induced oscillations (ERS) are dominant in the 10- to 13-Hz band and very likely mediated by thalamic gating. **Key Words:** Alpha band rhythms—Cortical inhibition—Thalamic gating—Event-related desynchronization (ERD)—Event-related synchronization (ERS).

EVENT-RELATED EEG (DE) SYNCHRONIZATION

One characteristic feature of the brain is its ability to generate rhythmic potentials or oscillatory activity. This fact was discovered as early as 1949 by Jasper and Penfield (1), who also discussed the relation between alpha and beta rhythms and their functioning in relation to underlying neuronal networks. The frequency of brain oscillations depends on both membrane properties of single neurons and the organization and interconnectivity of networks to which they belong (2). Such a network can either comprise a large number of neurons controlled by thalamocortical feedback loops or only a small number of neurons interconnected by intracortical feedback loops. Coherent activity in large neuronal pools can result in high-amplitude, low-frequency oscillations (e.g., alpha band rhythms), whereas synchrony in localized neuronal pools can be the source of gamma oscillations (3).

A neural network can display different states of synchrony whereby feedback loops can shape their dynamics and create oscillations in different frequency bands. The dynamic of such a network can result in phasic changes in the synchrony of cell populations due to externally or internally paced events and lead to characteristic EEG patterns. Two types of such patterns are observed, the event-related desynchronization or ERD in the form of an amplitude attenuation and the event-related synchronization or ERS in the form of an enhancement of specific frequency components (4). Such enhanced alpha oscillations are always time-locked to an event but can be either phase-locked (evoked) or not phase-locked (induced). Both evoked alpha oscillations (5) and induced ones (6–8) have been analyzed in detail.

One major difference between evoked and induced alpha oscillations is that only the former are of short duration (∼200–300 ms) and can be extracted from the ongoing EEG activity by simple linear methods such as averaging.

One of the basic features of ERD/ERS measurements is that the EEG power within an identified frequency band is displayed relative to the power of the same EEG derivation recorded during the reference or baseline period a few seconds before the event occurs. Because event-related changes in ongoing EEG need time to develop and to recover, especially when alpha oscillations are involved, the interval between two consecutive events should last at least some seconds.

The classic method to compute the time course of ERD/ERS includes bandpass filtering of all event-related trials, squaring of the amplitude samples to obtain power samples, averaging of power samples across all trials, and averaging over time samples to smooth the data and reduce the variability (4). 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 following expression:

$$\mathrm{ERD}\% = [(\mathrm{A} - \mathrm{R})/\mathrm{R}]100$$

Address correspondence and reprint requests to Dr. G. Pfurtscheller at Inffeldgasse 16a/II, A-8010 Graz, Switzerland. E-mail: pfu@dpmi.tugraz.ac.at

For spatial mapping of ERD/ERS, different methods are available as, for example, the calculation of surface laplacian, cortical imaging, and distributed source imaging (9).

ON THE EXISTENCE OF DIFFERENT RHYTHMS IN THE ALPHA BAND

A great variety of "alpha rhythms" exist, rather than a single one. This fact, known and mentioned by Grey Walter, was also documented recently by electrocorticographic recordings of the human cortex (10,11). In addition to the well-known occipital alpha rhythm (12) and the auditory tau rhythm (13), the rolandic mu rhythm (14,15) is of special interest. Face and foot area-specific mu rhythms have been reported (1,10), whereas conversely, converging evidence shows that at least two types of rolandic rhythms in the alpha frequency band can be distinguished. Both are blocked before and during movement and should therefore be considered mu rhythms, although their reactive frequency components are different.

The lower-frequency (8–10 Hz) mu rhythm shows a widespread movement-type–unspecific ERD pattern about similar for finger or foot movement, whereas the higher frequency (10–13 Hz) mu rhythm shows a more focused, movement-type–specific ERD pattern, clearly different with finger and foot movement (16). It also has been mentioned that factor analyses applied to spontaneous EEG under eyes-closed condition revealed a lower (9–10.5 Hz) and a higher (10.5–12.5 Hz) alpha band (17).

The desynchronization of lower mu components found over frontal, central, and parietal areas may indicate the existence of a distributed neural network in the sensorimotor cortex. This purported network is activated by different types of motor behavior, but it is not necessarily critical to support a specific movement. This system may act as a relatively nonspecific activation or presetting of somatosensory and motor neurons in cortical movement representation areas before a specific motor act. Another interpretation could be a neurophysiologic mechanism that serves for general motor attention to all cortical areas involved in a motor task including premotor and parietal areas in addition to primary sensorimotor. Lower alpha desynchronization is also obtained in response to a variety of non–task-specific factors that may be best summed up under the term "attention." This ERD is topographically widespread over the scalp and probably reflects general task demands and attentional processes (18). It is not unlikely that similar neurophysiologic mechanisms operate in the lower alpha band during cognitive and motor processing.

In contrast to the widespread and somatotopically unspecific desynchronization of the lower-frequency mu rhythm, the desynchronization of upper mu components is somatotopically specific, topographically restricted, and starts with unilateral voluntary hand movement ~2 s before movement onset over the contralateral hand area (19). A similar higher alpha frequency desynchronization with a topographic restriction during processing of sensory semantic information also has been reported (18).

FOCAL ERD/SURROUND ERS

The term "focal ERD/surround ERS" was introduced to describe the observation that blocking or desynchronization of rhythmic activity in the alpha band does not occur in isolation but can be accompanied by an amplitude increase or synchronization in neighboring cortical areas that correspond to the same or to another modality of information processing (20).

An intermodal interaction in form of a central desynchronization and a parietooccipital synchronization that is characteristic for voluntary finger movement in the alpha band can be seen in raw EEG data (Fig. 1) and also visualized in form of maps (Fig. 2A). The opposite phenomenon (i.e., enhancement of central mu rhythm and blocking of occipital alpha rhythms during visual stimulation) also has been reported (21–23).

A further example of focal ERD/surround ERS obtained with a dense EEG electrode montage demonstrating hand-area ERD and foot-area ERS during hand movement and hand-area ERS and foot-area ERD during foot movement is illustrated in Fig. 2B.

The focal mu desynchronization in the 10- to 13-Hz band as documented in Fig. 2 may reflect a mechanism responsible for selective attention focused to a motor subsystem. This effect of selective attention may be accentuated when other cortical areas, not directly involved in the specific motor task (e.g., parietooccipital areas), are "inhibited." Increased alpha synchronization over posterior regions may reflect a reduced capacity of information processing in underlying neuronal networks (8). In contrast, the desynchronised mu rhythm during the motor task indicates facilitation of information processing through hand-area networks.

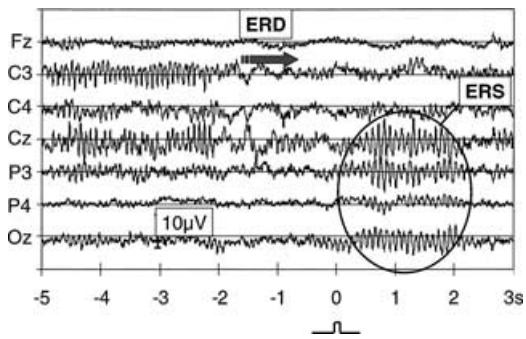

FIG. 1. Examples of ongoing EEG data recorded during right-finger movement. Movement onset at t = 0 s. Note the EEG desynchronization at electrode location C3, starting ~1.5 s before movement-onset and the induced alpha band oscillatory (ERS) over the posterior region during movement. ERD, event-related desynchronization. (Modified from ref. 4, with permission.)

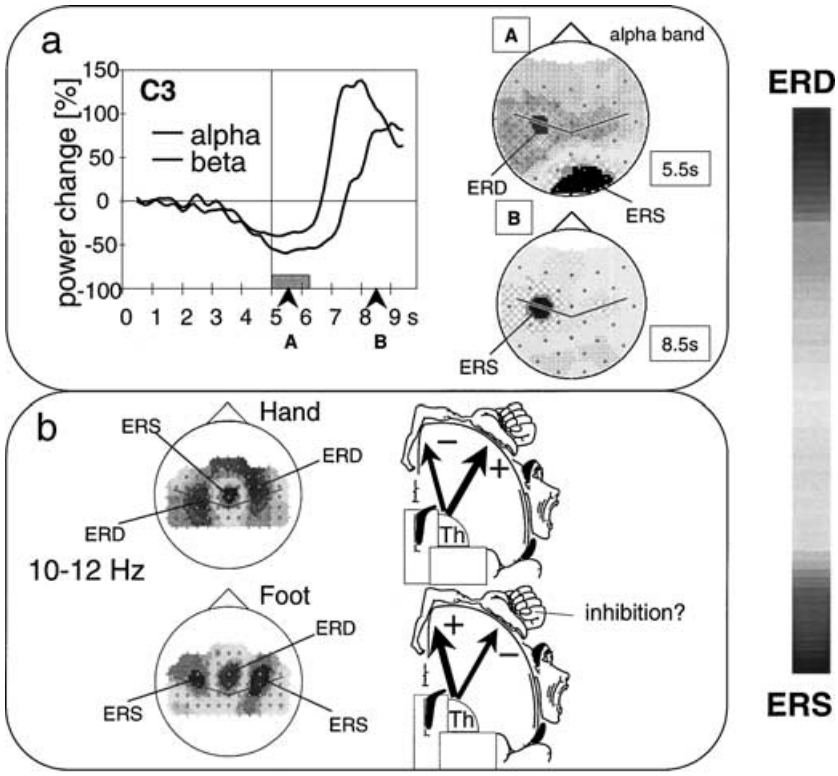

FIG. 2. **a:** Grand average (N = 9) event-related desynchronization (ERD)/event-related synchronization (ERS) curves calculated in the alpha and beta bands in a right-hand movement task **(left side)**. Grand average maps calculated for a 125-ms interval during movement (bar A above arrowhead) and after 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**. Power decrease or ERD; power increase or ERS. (Modified from ref. 4, with permission.)

A similar antagonistic behavior involving desynchronization of central mu rhythm and synchronization of parietooccipital alpha rhythms during repetitive brief finger movement has been reported by others (24). A task-related power increase found in the 9- to 11-Hz band can be interpreted as possibly reflecting an "inhibitory state" of occipital and parietooccipital regions, because no visual feedback was presented.

Furthermore, paradoxical alpha enhancement over parietal regions during preparation of self-paced fist closing, dominant during eyes-opened condition, was identified (25). This parietal alpha increase was found to coincide with a central decrease of activity in the 8- to 12-Hz band (mu ERD). The preservation of this alpha increase or alpha ERS in the premovement period differs from our findings of an alpha increase starting after movement onset (16). Nevertheless, it confirms that a mu rhythm ERD can be, at least under certain circumstances, accompanied by an alpha ERS over parietal regions.

The enhancement of parietooccipital rhythms is frequency band specific, dominant in the higher alpha band (Fig. 3), and found with self-paced voluntary hand but not with foot movement (16). The latter can be the result of a mechanism withdrawing attention from the visual system and facilitating selective attention on the motor subsystem supporting hand/finger movements.

The hand area has a greater functional importance than the foot area and therefore has a higher energy demand during activation. The relevant hypothesis here is that the increase of neuronal activity in the hand area is compensated by a decreased activity in parietooccipital areas.

SELF-PACED MOVEMENT VERSUS CUE-PACED MOVEMENT

Execution of self-paced hand movement in intervals of ~10 s is accompanied by a contralateral dominant mu ERD in both the higher and the lower alpha bands. Self-paced foot movements executed one after the other in intervals of a few seconds results in a widespread ERD in the 6- to 10-Hz range (26). In this case, no characteristic change over the hand area in the higher alpha band was found (16). However, when the same types of movement (i.e., either a hand or a foot movement) have to be made cue dependent, the intrinsic activity of the hand area shows an antagonistic behavior in the 10- to 13-Hz band. Thus, hand movement results in a decrease of rhythmic activity or ERD similar to that of consecutive self-paced hand movements, whereas foot movement is accompanied by a power increase or ERS in the 10- to 13-Hz frequency range (27) (Fig. 4). One explanation for this phenomenon may be that before the cue-stimulus ordering the extremity (hand or foot) to carry out a movement, various sensorimotor areas, including those representing the hand and the foot, are preactivated or primed and therefore transferred in a state of increased excitability. Characteristic for such a cortical state are slow negative potential shifts, such as the contingent negative variation (CNV) as first described

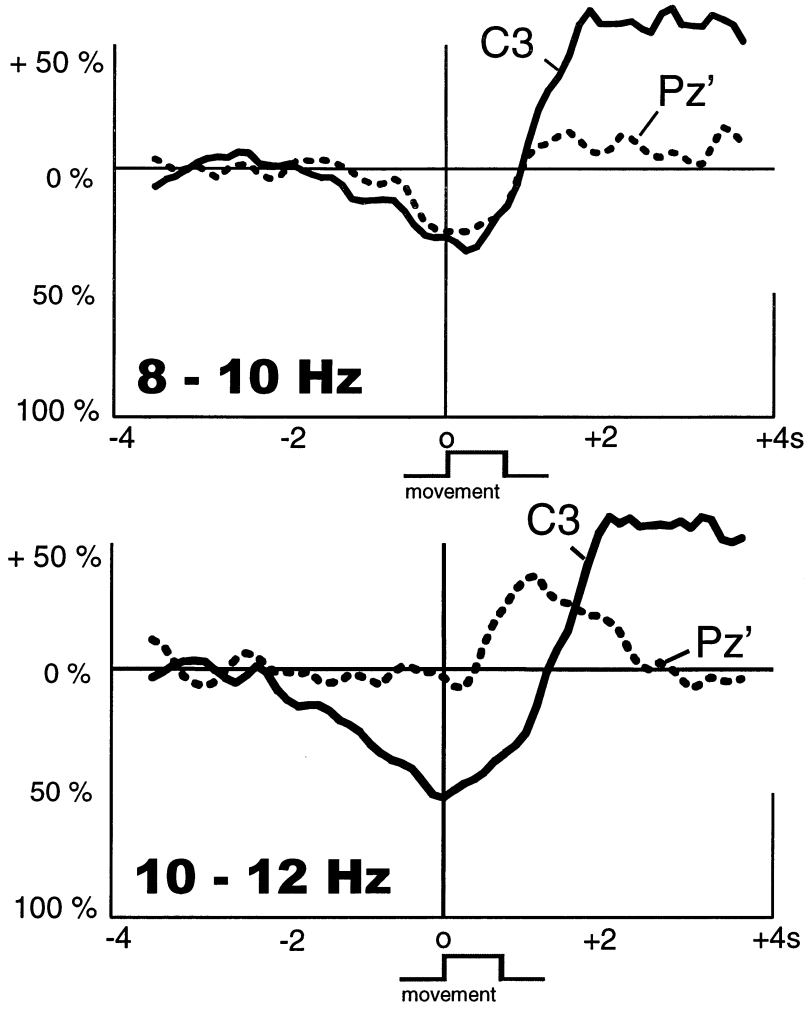

FIG. 3. Grand average event-related desynchronization (ERD)/event-related synchronization curves recorded at central (C3) versus parietal (Pz') electrode locations during voluntary finger movement. Data are provided in the 8- to 10-Hz **(upper)** and 10- to 12-Hz bands **(lower)**. Horizontal line, the level of reference band power; vertical line, the onset of movement; downward deflection, band power decrease or ERD. (Modified from ref. 16, with permission.)

by Grey Walter (28), and, concurrently, a desynchronized EEG pattern (29). When the cue-stimulus indicates "foot movement," the hand-area preactivation has to be "inhibited," whereas the foot-area preactivation is facilitated (see also Fig. 5). This "inhibition" of the hand-area network is time-locked to induced oscillations in the higher alpha band and topographically restricted to electrodes overlaying the hand area.

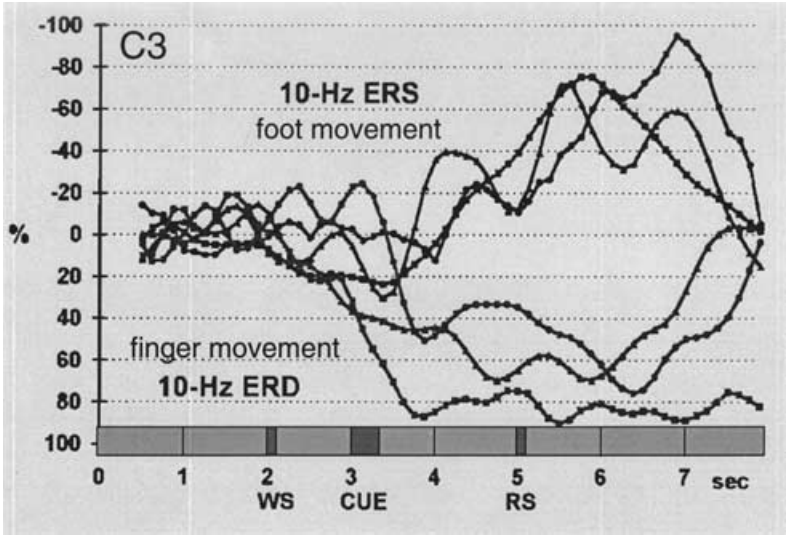

FIG. 4. Event-related desynchronization (ERD)/event-related synchronization (ERS) time courses (10–12 Hz) of three subjects display percentage power decrease (10-Hz ERD) during finger movement and power increase (10-Hz ERS) during foot movement over the primary hand area (electrode C3). WS, warning stimulus; CUE, cue stimulus; RS, reaction stimulus. (Modified from ref. 27, with permission.)

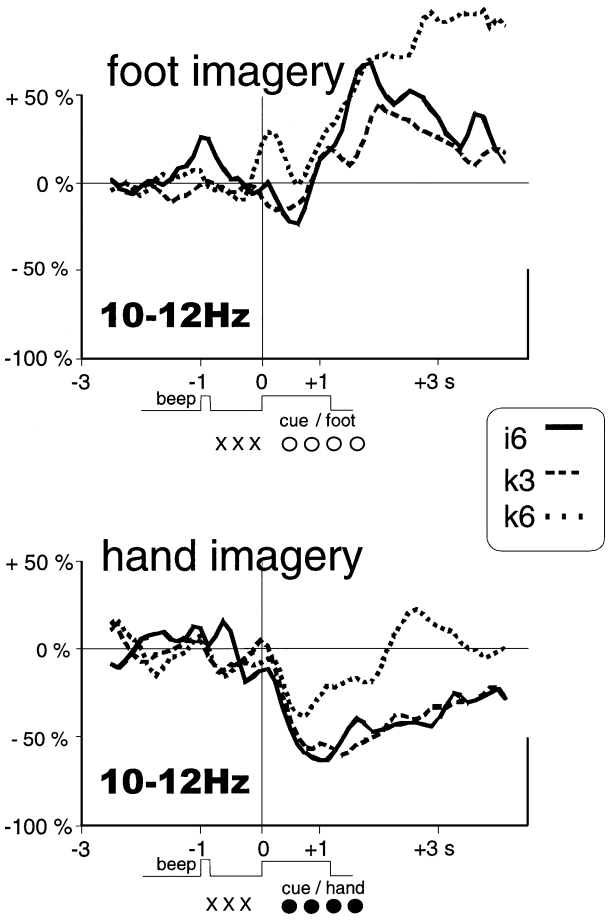

FIG. 5. Event-related desynchronization (ERD)/event-related synchronization time courses (10–12 Hz) of three subjects (i6, K3, K6) from movement imagery experiments (right hand versus foot) recorded from electrode position C3. Imagination of foot movement induces alpha oscillations (10–12 Hz) over the primary hand area (electrode position C3). Imagination of hand movement results in a 10-Hz ERD. xxx, Period during which subjects expect the forthcoming cue stimulus; °°°, time of foot-movement imagery; •••, time of hand-movement imagery.

This antagonistic behavior of alpha components (ERD/ERS) is a dominant feature of the higher alpha band, not seen with lower-frequency components, and found both for real and imagined movements. Another example of induced alpha oscillations in the hand area from a motor imagery task is shown in Fig. 5.

THALAMIC GATING

Strong evidence indicates that alpha spindles in sleep are controlled by interplay between thalamic relay cells (TRCs) and the thalamic reticular nucleus (RE). The latter forms a topographically organized inhibitory feedback mechanism that is capable of controlling the information flow through the thalamus (2,30). The TRCs and RE cells show two basic modes of activity, the tonic mode and the burst-firing mode. The tonic (relay) mode is associated with a desynchronized EEG and an "open" thalamic gate by which sensory information is transferred to the cortex. When spindles are present during the burst mode, the membrane potential of TRCs is hyperpolarized, and the thalamic gate is "closed." Although these thalamic modes can be applied only to spindle activity occurring during sleep, strictly speaking, we assume that the frequency of oscillations characteristic for sleep spindles in the range 7–14 Hz (2) and the induced alpha oscillations within the 10- to 13-Hz band in the awake state share the same basic mechanism of the thalamocortical gating.

The concept of thalamic gating is not new. A central gating mechanism in the thalamus regulates cortical negative shifts and EEG desynchronization during attentive behavior (31). Even before that, it has been known that long-duration inhibitory postsynaptic potentials (IPSPs) in thalamic cells (burst mode) are the basic element underlying cortical synchronization or spontaneous spindles (32). The thalamic gating is closely related to the proposed process of selective attention (31,33–35). The selection process focused on visual attention has been called a "searchlight" (34), whereas others dealt with an abstract attention model simulating the relative enhancement of input information (35).

The new concept for the thalamic gating model is the introduction of a type of "lateral inhibition," as documented by the induced alpha in the awake state. We hypothesize that a focal cortical activation due to an open gate can be accompanied by a deactivation or inhibition of other (surrounding) cortical areas due to closed gates (Fig. 6). This "surround ERS" could be a mechanism to facilitate the processing in a specific cortical area. The effect of focal attention can be accentuated by "active inhibition" of surrounding areas.

Based on a lumped neuronal model (36), the interplay of TRCs and RE cells was simulated, whereby not only two modules, each consisting of a population of TRCs and RE cells, but also a number of modules corresponding to the chain of mutually interconnected RE cells, were used (20). The model is able to simulate focal ERD/surround ERS and supports the hypothesis that a closed gate can be accompanied by induced spindle-like alpha oscillations in the range of 10–13 Hz.

CONCLUSION

Two conclusions can be made based on the data reported in the last sections:

a. One cortical area (e.g., hand-representation area on the sensorimotor strip) can display three types of event-related alpha patterns [i.e., no appreciable EEG changes, an alpha (mu) desynchronization (10-Hz ERD), or induced alpha (mu) oscillations (10-Hz ERS)].
b. Both phenomena, event-related desynchronization and synchronization in the alpha band, can be

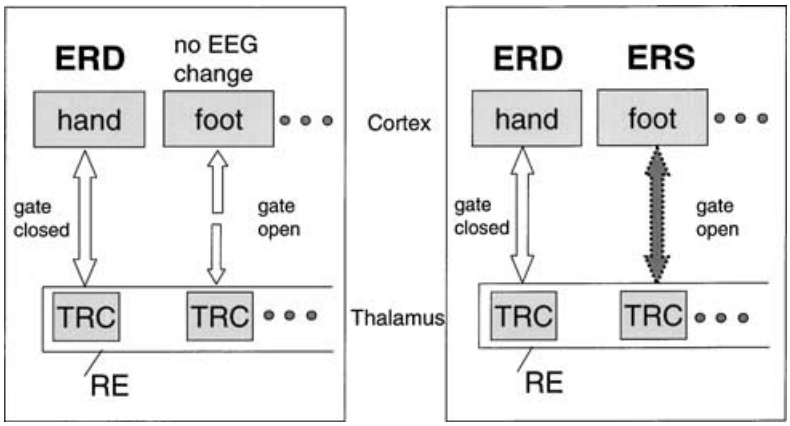

FIG. 6. Simplified models for thalamic gating. **Left:** An open gate results in a "focal event related desynchronization (ERD)," and a closed gate, in no detectable EEG changes. **Right:** An open gate results in a "focal ERD" in the activated module, and a closed gate induces oscillations in other modules ["surround event-related synchronization (ERS)"]. TRC, thalamic relay cell; RE, thalamic reticulus nucleus.

found simultaneously on different scalp locations, demonstrating either intermodal or intramodal interactions.

From (a), it follows that not only single neurons, but also neural networks in the cortex composed of interconnected excitatory and inhibitory neurons, can be in one of three states (resting, depolarized, or hyperpolarized). One state would be dominated by a depolarization of cell membranes and as a consequence of increased excitability of cortical neurons with the capability of facilitating information processing. This state is characterized by a 10-Hz ERD. Another state (10-Hz ERS) would be associated with a decreased excitability of cortical neurons and depressed or even blocked information-processing capabilities. The third state of a neural network is the resting (or quiescent) state with neither enhanced nor reduced excitability levels.

It is important to differentiate between "cortical nilwork" (37) or "cortical idling" (8,38,39), and a deactivated or inhibited cortical area. The term "idling" was first used to describe large-amplitude alpha rhythms emerging in the cortex in the absence of a stimulus (38). In this sense, the occipital alpha and the central mu rhythms were considered idling rhythms of the corresponding cortical projection area (40). In contrast to these long-lasting idling rhythms occurring in the whole alpha range, the task-related induced alpha oscillations are short lasting, dominant in the 10- to 13-Hz band, and can be interpreted as a correlate of an inhibited cortical network.

The induced spindle-like alpha oscillations in the awake state are in a frequency range (7–14 Hz) similar to that of sleep spindles. Such spindles appear in the early stages of sleep and are associated with a blockade of synaptic transmission through the thalamus (41). It can be speculated that a part of the TRCs becomes hyperpolarized and contributes to a burst-like mode with a blockade of thalamocortical information transfer, not only in sleep, but also during wakefulness. The antagonistic ERD/ERS pattern may therefore be seen as a result of a thalamocortical mechanism enhancing focal cortical activation (focal ERD) by a simultaneous deactivation or inhibition of other cortical areas (surround ERS) similar to the mechanism of lateral inhibition in the retina.

REFERENCES

1. Jasper H, Penfield W. Electrocorticograms in man: effect of voluntary movement upon the electrical activity of the precentral gyrus. *Arch Psychiatr Z Neurol* 1949;183:163–74.
2. Lopes da Silva FH. Neural mechanisms underlying brain waves: from neural membranes to networks. *Electroencephalogr Clin Neurophysiol* 1991;79:81–93.
3. Lopes da Silva FH, Pfurtscheller G. Basic concepts on EEG synchronization and desynchronization. In: Pfurtscheller G, Lopes da Silva FH, eds. *Event-related desynchronization: handbook of electroencephalography and clinical neurophysiolog*, rev. ed. Amsterdam: Elsevier, 1999:3–11.
4. Pfurtscheller G, Lopes da Silva FH. Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol* 1999;110:1842–57.
5. Basar E, Schürmann M, Başar-Eroglu C, et al. Alpha oscillations in brain functioning: an integrative theory. *Int J Psychophysiol* 1997;26:5–29.
6. Morrell LK. Some characteristics of stimulus-provoked alpha activity. *Electroencephalogr Clin Neurophysiol* 1996;21:552–61.
7. Nagawa T, Katayama K, Tabata Y, et al. Changes in amplitude of the EEG induced by a photic stimulus. *Electroencephalogr Clin Neurophysiol* 1976;40:78–88.
8. Pfurtscheller G. Event-related synchronization (ERS): an electrophysiological correlate of cortical areas at rest. *Electroencephalogr Clin Neurophysiol* 1992;82:62–9.
9. Van Burik M, Edlinger G, Pfurtscheller G. Spatial mapping of ERD/ERS. In: Pfurtscheller G, Lopes da Silva FH, eds. *Event-related desynchronization: handbook of electroencephalography and clinical neurophysiology*, rev. ed. Amsterdam: Elsevier, 1999:107–18.
10. Arroyo S, Lesser RP, Gordon B, et al. Functional significance of the mu rhythm of human cortex: an electrophysiologic study with subdural electrodes. *Electroencephalogr Clin Neurophysiol* 1993;87:76–87.
11. Crone NE, Miglioretti DL, Gordon B, et al. Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis, I: alpha and beta event-related desynchronization. *Brain* 1998;121:2271–99.
12. Berger H. Über das Elektrenkephalogramm des Menschen. *Arch Psychiatr Nervenkr* 1933;100:301–20.
13. Tiihonen J, Hari R, Kajola M, et al. Magnetoecephalographic 10 Hz rhythm from the human auditory cortex. *Neurosci Lett* 1991;129:303–5.
14. Chatrian GE, Peterson MC, Lazarte JA. The blocking of the rolandic wicket rhythm and some central changes related to movement. *Electroencephalogr Clin Neurophysiol* 1959;11:497–510.

15. Gastaut H. Étude électrocorticographique de la reactivité des rhythmes rolandiques. *Rev Neurol* 1952;87:176–82.
16. Pfurtscheller G, Neuper C, Krausz G. Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement. *Clin Neurophysiol* 2000;111:1873–9.
17. Lopes da Silva FH. Dynamics of EEGs as signals of neuronal populations: models and theoretical considerations. In: Niedermeyer E, Lopes da Silva FH, eds. *Electroencephalography: basic principles, clinical applications and related fields.* 3rd ed. Baltimore: Williams & Wilkins, 1993:63–77.
18. Klimesch W. Event-related band power changes and memory performance. In: Pfurtscheller G, Lopes da Silva FH, eds. *Event-related desynchronization: handbook of electroencephalography and clinical neurophysiology*, rev. ed. Amsterdam: Elsevier, 1999:161–78.
19. Pfurtscheller G, Pichler-Zalaudek K, Neuper C. ERD and ERS in voluntary movement of different limbs. In: Pfurtscheller G, Lopes da Silva FH, eds. *Event-related desynchronization: handbook of electroencephalography and clinical neurophysiology*, rev. ed. Amsterdam: Elsevier, 1999:245–68.
20. Suffczynski P, Pijn PJM, Pfurtscheller G, et al. Event-related dynamics of alpha band rhythms: a neuronal network model of focal ERD/surround ERS. In: Pfurtscheller G, Lopes da Silva FH, eds. *Event-related desynchronization: handbook of electroencephalography and clinical neurophysiology*, rev. ed. Amsterdam: Elsevier, 1999:6:67–85.
21. Koshino Y, Niedermeyer E. Enhancement of rolandic mu-rhythm by pattern vision. *Electroencephalogr Clin Neurophysiol* 1975;38:535–8.
22. Kreitmann N, Shaw JC. Experimental enhancement of alpha activity. *Electroencephalogr Clin Neurophysiol* 1965;18:147–55.
23. Pfurtscheller G, Klimesch W. Cortical activation pattern during reading and recognition of words studied with dynamic event-related desynchronization mapping. In: Maurer K, ed. *Topographic brain mapping of EEG and evoked potentials*. Berlin: Springer, 1989:303–13.
24. Gerloff C, Hadley J, Richard J, et al. Functional coupling and regional activation of human cortical motor areas during simple, internally paced and externally paced finger movements. *Brain* 1998;121:1513–31.
25. Westphal KP, Grözinger B, Diekman V, et al. EEG-blocking before and during voluntary movements: differences between the eyes-closed and the eyes-open condition. *Arch Ital Biol* 1993;131:25–35.
26. Neuper C, Pfurtscheller G. Post-movement synchronization of beta rhythms in the EEG over the cortical foot area in man. *Neurosci Lett* 1996;216:17–20.
27. Pfurtscheller G, Neuper C. Event-related synchronization of mu rhythm in the EEG over the cortical hand area in man. *Neurosci Lett* 1994;174:93–6.
28. Walter WGR, Cooper R, Aldridge VJ, et al. Contingent negative variation: an electrical sign of sensorimotor association and expectancy in the human brain. *Nature* 1964;203:380–4.
29. Neuper C, Pfurtscheller G. Ereignisbezogene Negativierung und Alphaband-Desynchronisationen bei motorischen Reaktionen. *Z EEG-EMG* 1992;23:55–61.
30. Steriade M, Llinas R. The functional states of the thalamus and the associated neuronal interplay. *Physiol Rev* 1988;68:649–742.
31. Skinner JE, Yingling CD. Central gating mechanisms that regulate event-related potentials and behavior. In: Desmedt JE, ed. *Attention, voluntary contraction and slow potential shifts*. Basel: Karger, 1977:30–69.
32. Andersen P, Eccles JC. Inhibitory phasing of neuronal discharge. *Nature* 1962;196:645–7.
33. Brunia CHM. Neural aspects of anticipatory behavior. *Acta Psychol* 1999;101:213–42.
34. Crick F. The function of the thalamic reticular complex: the searchlight hypothesis. *Proc Natl Acad Sci U S A* 1984;81:4586–90.
35. LaBerge D, Carter M, Brown V. A network simulation of thalamic circuit operations in selective attention. *Neural Comput* 1992;4:318–31.
36. Lopes da Silva FH, Hoeks A, Smits H, et al. Model of brain rhythmic activity: the alpha-rhythm of the thalamus. *Kybernetic* 1974;15:27–37.
37. Mulholland T. Human EEG, behavioral stillness and biofeedback. *Int J Psychophysiol* 1995;19:263–79.
38. Adrian ED, Matthews BHC. The Berger rhythm: potential changes from the occipital lobes in man. *Brain* 1934;4:355–85.
39. Chase MH, Harper RM. Somatomotor and visceromotor correlates of operantly conditioned 12-14 Hz sensorimotor cortical activity. *Electroencephalogr Clin Neurophysiol* 1971;31:85–92.
40. Kuhlman WN. Functional topography of the human mu rhythm. *Electroencephalogr Clin Neurophysiol* 1978;44:83–93.
41. Steriade M, McCormick DA, Sejnowski TJ. Thalamocortical oscillations in the sleeping and aroused brain. *Science* 1993;262:679–85.