



# Human cortical oscillations: a neuromagnetic view through the skull

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**The mammalian cerebral cortex generates a variety of rhythmic oscillations, detectable directly from the cortex or the scalp. Recent non-invasive recordings from intact humans, by means of neuromagnetometers with large sensor arrays, have shown that several regions of the healthy human cortex have their own intrinsic rhythms, typically 8–40 Hz in frequency, with modality- and frequency-specific reactivity. The conventional hypotheses about the functional significance of brain rhythms extend from epiphenomena to perceptual binding and object segmentation. Recent data indicate that some cortical rhythms can be related to periodic activity of peripheral sensor and effector organs.**

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NEURONES IN THE HUMAN BRAIN, especially in thalamic nuclei and in the cerebral cortex, exhibit intrinsic oscillations<sup>1–3</sup>, which probably form the basis for macroscopic rhythms, detectable with electroencephalography (EEG) and magnetoencephalography (MEG). Analysis of cortical rhythms forms an essential part of clinical EEG evaluation, which relies on correlations between the signal phenomenology and brain disorders. However, despite extensive animal experiments<sup>2,4</sup>, the functional significance of cortical rhythms has remained largely unknown.

Interest in human brain rhythms started to increase with the development of neuromagnetometers with extended sensor arrays. MEG (Refs 5–9), although closely related to EEG, benefits from the transparency of the skull and the scalp to magnetic fields: the MEG signals, which arise mainly from synaptic currents in fissural cortex, can be picked up outside the head undisturbed by tissue inhomogeneities. MEG thus provides a non-invasive view ‘through the skull’ on temporospatial activation patterns of the human cerebral cortex (Fig. 1). Early attempts to localize the sources of spontaneous brain rhythms already offered some insights into the function of the active brain regions<sup>12–14</sup>, but were handicapped by the small coverage of the MEG sensor arrays. Only the recent emergence of whole-scalp magnetometers has made studies of spontaneous activity of the whole human neocortex feasible.

The best known electric oscillations of the human brain are the alpha rhythm, detected with EEG over the posterior parts of the brain<sup>15–17</sup>, and the mu rhythm, recorded over the rolandic regions<sup>18,19</sup>. Both rhythms are seen clearly in MEG recordings (see Fig. 1) and display modality-specific reactivity: the posterior rhythm is dampened by opening the eyes, and the rolandic rhythm is dampened by limb movements and tactile stimulation. A third modality-specific MEG rhythm, ‘tau’, has been recorded from the supratemporal auditory cortex. It increases during drowsiness and is occasionally dampened by sounds<sup>8,20,21</sup>.

## Source modelling

The invasive microelectrode recordings have the advantage that the neuronal structure generating the

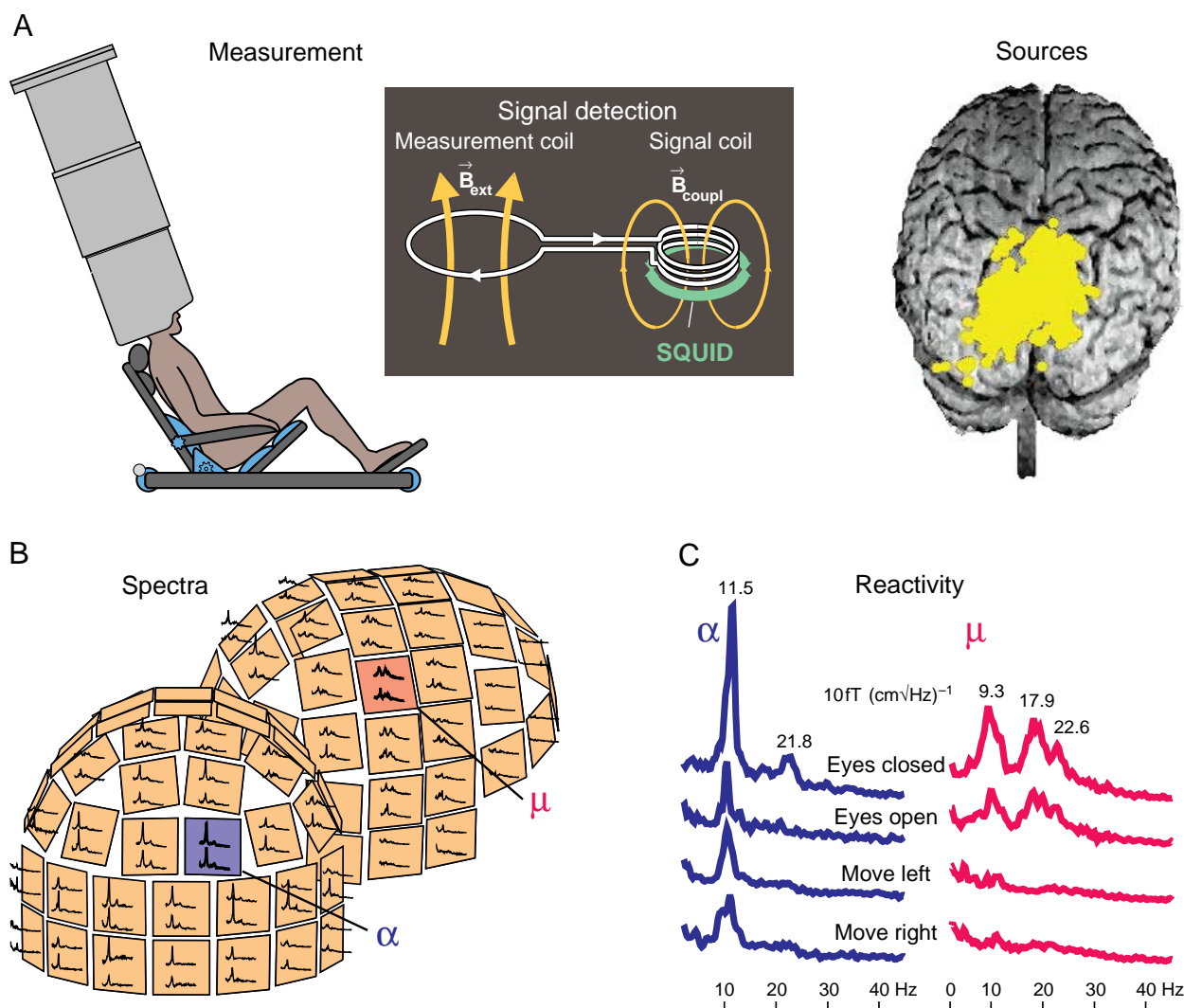
signals can be identified easily. By contrast, MEG (and EEG) sensors pick up signals from extensive brain regions, which might be even several centimetres away from the sensor. Therefore the sites of active neuronal populations have to be deduced from the measured signal distribution. Although this ‘inverse problem’ does not have a unique solution in the general case<sup>6,9</sup>, modelling the generators of MEG signals as current dipoles allows identification of the most probable source areas. A current dipole describes a local active cortical area well, and can also be used to represent the centre of gravity of an extended active brain region<sup>8</sup>. For elicited responses, sources are typically modelled during peaks of the responses to benefit from the best signal-to-noise ratio. Owing to the spatial complexity and temporal overlap of active cortical areas, magnetic field patterns of brain rhythms might be strictly dipolar only during 1–3% of typical analysis intervals, selected on the basis of visually identifiable oscillatory activity<sup>11,22</sup>.

Figure 1A (right) illustrates a source cluster for the posterior 10 Hz rhythm, obtained by determining the model parameters at 5–10 ms intervals over several tens of seconds; the cluster gives an estimate for the active brain region, but it is also affected by noise and thus has to be considered as a statistical representation of the most probable source areas. In this figure, the sources have been projected to the surface of the brain for illustrative purposes; the current orientations, typically perpendicular to the course of cortical fissures, are not shown. Sources can also be defined readily in frequency domain<sup>23–25</sup>, although the approach is only selectively applicable for physiological studies of brain oscillations, which are not strictly periodic and typically occur in brief bursts. A recent review<sup>9</sup> can be consulted for detailed description of the MEG data interpretation.

## Sources and reactivity of the alpha rhythm

Sources of the posterior 10 Hz alpha rhythm concentrate predominantly in the parieto-occipital region and, to a smaller extent, in the occipital areas. The two subclusters differ both by their sites and current orientations, and suggest that the strongest activity

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**Fig. 1. Recording and displaying of magnetoencephalographic rhythms.** (A) (Left) The subject sits in a magnetically shielded room, with his head under a whole-scalp neuromagnetometer, which houses 122 superconducting SQUIDs (superconducting quantum interference devices) on a helmet-like sensor array<sup>10</sup>. (Middle) The external magnetic flux, generated by currents flowing in the human brain, penetrates the superconducting flux transformers. The resulting currents in the coils then couple the signal magnetically to the SQUID. (Right) A source cluster of the posterior 10 Hz oscillations superimposed on the surface rendering of the subject's brain, constructed from the magnetic resonance images. (B) Amplitude spectra of one subject calculated from a 1 min period of spontaneous activity when the subject was resting with the eyes closed. Each sensor unit records the changes of the radial magnetic field in two orthogonal directions along the plane of the helmet. (C) Reactivity of the parieto-occipital ('alpha') and rolandic ('mu') rhythms to opening of the eyes and to movements of the left and right hand. The MEG data are adapted from Ref. 11.

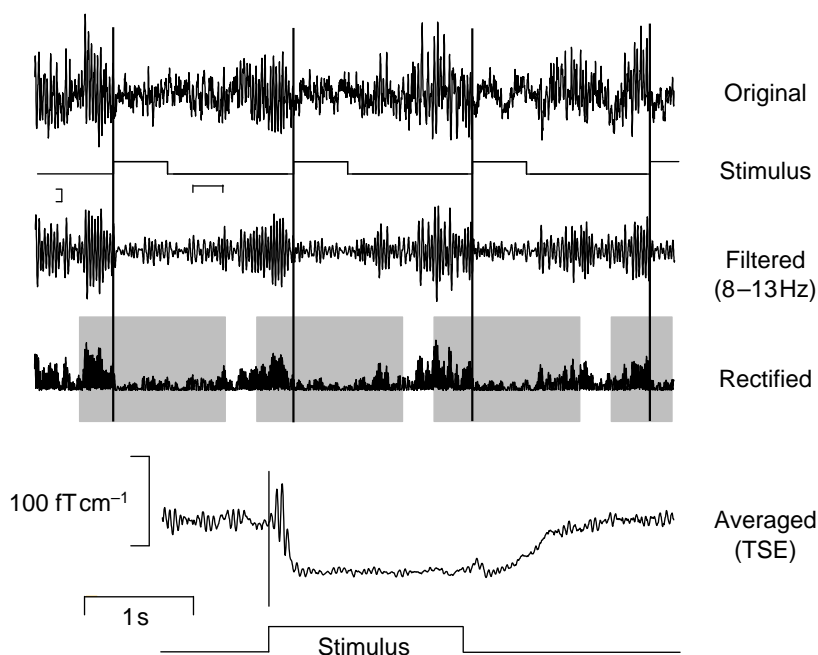
occurs in the parieto-occipital sulcus with less activity in the calcarine sulcus<sup>22,26</sup>. Even within these sub-clusters, several single sources with independent time behaviour might be active simultaneously<sup>11</sup>, thereby supporting previous studies that suggest a multitude of distinct sources for the electric and magnetic alpha oscillations<sup>27,28</sup>. The observed dominance of the parieto-occipital magnetic activity seems to contrast with the animal data<sup>29</sup>, which emphasize the role of the visual projection cortex in the generation of alpha activity. We assume that either the human calcarine region produces considerably less alpha-range activity than the parieto-occipital sulcus region, or the opposite orientations of source currents in the walls of calcarine fissures result in cancellation of the external magnetic field. The present data do not allow a distinction between these two possibilities.

The level of the posterior 10 Hz alpha rhythm decreases during and after visual stimulation (Fig. 2). Whereas stimulus-locked elicited responses typically concentrate within a time window of 0.5 s, cortical rhythms are modulated over periods of a few seconds.

In addition to the physical features of the stimuli, the reactivity also depends on the subject's performance and effort. For example, the phasic alpha suppression during passive viewing of pictures is intensified considerably when the subject is asked to name the pictures, either silently or aloud<sup>32</sup>.

Interestingly, changes very similar to those elicited by visual stimuli can also be produced by visual imagery. Figure 3 shows changes of the 10 Hz alpha rhythm during a visual letter-imagery task when the subject kept her eyes closed; the suppression reached its maximum within 1 s after the auditory presentation of a letter that the subject was to view in her mind's eye<sup>22</sup>. The suppression was strong also when the subject subsequently inspected the mental image to answer a probe question about its visual properties. In this type of experiment, the inter-individual variability is large, both in the brain's reactivity and in the subject's capability to form mental images.

These results suggest strong involvement of non-primary visual areas in the vicinity of the parieto-occipital sulcus in generation and inspection of mental



**Fig. 2. Monitoring the level of spontaneous activity.** The principle of TSE (temporal spectral evolution) analysis<sup>30</sup>, a method closely related to monitoring of signal power<sup>31</sup>. Spontaneous signals were recorded from the posterior part of the head when the subject was viewing pictures, appearing for 1.8 s once every 5.8 s. The original signal is first filtered, then rectified, and finally averaged (the shadowed areas indicate the averaged epochs). The resulting TSE curve (bottom) gives the average amplitude level of the frequency band of interest as a function of time with respect to the stimulus. Modified from Ref. 26.

images. The involvement of this brain region agrees with data from a recent study using positron emission tomography that shows activation of the mesial parietal cortex (precuneus) in association with memory-related imagery<sup>33</sup>. The reactivity of this area during visual imagery might reflect the close connections of the posterior parietal cortex to the prefrontal cortex, which houses the neuronal machinery necessary for working memory<sup>34</sup>.

It is worth mentioning that in previous MEG studies the region of the posterior parietal cortex close to the midline, which produces the prominent magnetic alpha activity, has shown strong activation after

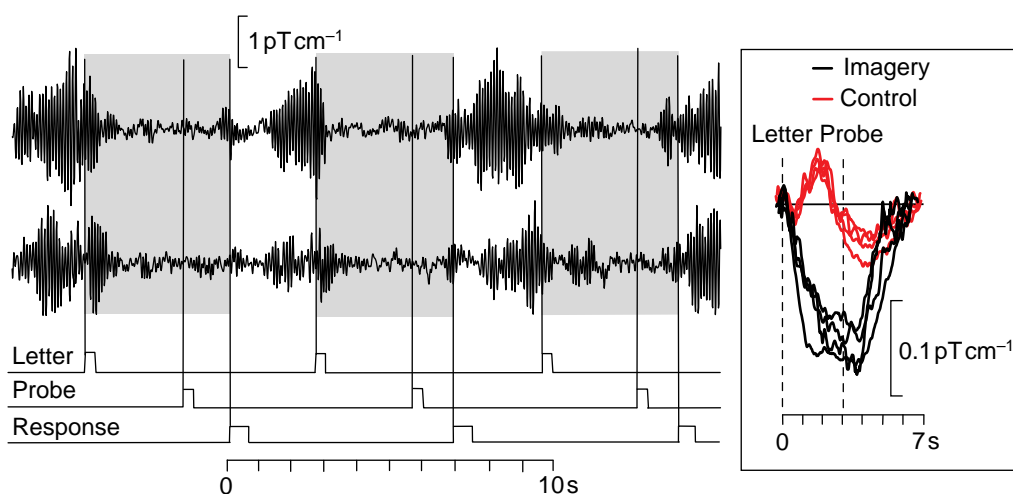
various visual stimuli<sup>35</sup> and in association with voluntary eye blinks<sup>36</sup> and saccades<sup>37</sup>. Anatomically, this area could be the human homologue of the monkey V6/V6A region, influenced by, for example, saccades and eye position, and hypothesized to be related to spatial coding of extrapersonal visual space and to visuomotor integration<sup>38,39</sup>.

### Segregation of the 10 Hz and 20 Hz somatomotor rhythms

The well-known 'comb-like' shape of the somatomotor mu rhythm implies that the rhythm consists of two or three frequency components with a nearly harmonic relationship. The dominant magnetic components near 10 Hz and 20 Hz (cf. Fig. 1) can occur either separately or simultaneously<sup>14</sup>, suggesting that the 20 Hz activity can be phase-locked to the 10 Hz rhythm at certain moments (and thus probably arise from the same neural generator) but stay totally independent at some other moments of time. Both frequency bands react with a rebound to the offset of a brisk movement, but the rebound is about 0.3 s faster and much stronger for the 20 Hz than for the 10 Hz signals<sup>30</sup>; a similar trend was evident in previous EEG data<sup>40</sup>.

The human magnetic mu rhythm observed during rest originates close to the primary somatosensory cortex for the hand<sup>14,30</sup>. This localization might be related to the large representation of the hand, especially the thumb, in the somatosensory homunculus, reflecting the importance of the hand in human behaviour. Interestingly, the sources of the 20 Hz component cluster anterior to those of the 10 Hz component with respect to the course of the central sulcus<sup>30</sup>, suggesting that they receive contribution from the precentral motor cortex. Similar segregation has been observed previously in direct recordings from the human cortex<sup>41,42</sup>, and is also evident in cats and monkeys<sup>43</sup>.

The observed differences naturally raise the question whether the 10 Hz and 20 Hz rhythms might be differently related to body movements. This was studied recently<sup>44</sup> in eight healthy subjects by identifying source locations during the rebounds after movements. For



**Fig. 3. Effect of visual imagery on parieto-occipital alpha rhythm.** Reactivity of the parieto-occipital 10 Hz alpha during a letter-imagery task. Names of letters and questions about them (probes) were presented auditorily; the subject reacted by lifting an index finger. The inset shows the level [temporal spectral evolution (TSE) curves] of the 7–14 Hz posterior rhythm during imagery and control tasks, both repeated four times; each trace is the average of about 60 single responses. Modified from Ref. 22.

10 Hz rhythms, the sources clustered close to the hand region, extending well into the postcentral cortex, regardless of the body part moved. By contrast, the sources of the 20 Hz rhythms followed the somatotopic organization of the body parts along the precentral gyrus, shifting from the most medial position for foot movements via the hand area to the most lateral location for mouth movements (Fig. 4). The dissociation of source locations, as well as the different timing and strength of the rebounds, suggest strongly that the two frequency components of the somatomotor rhythms are related to separate functional networks: the 10 Hz rhythm reflects predominantly somatosensory cortical function, and the 20 Hz rhythm is associated more with motor cortical function. Interestingly, the 20 Hz

component is also modified when the subject imagines exploratory finger movements<sup>45</sup>, indicating involvement of the primary motor cortex in motor imagery.

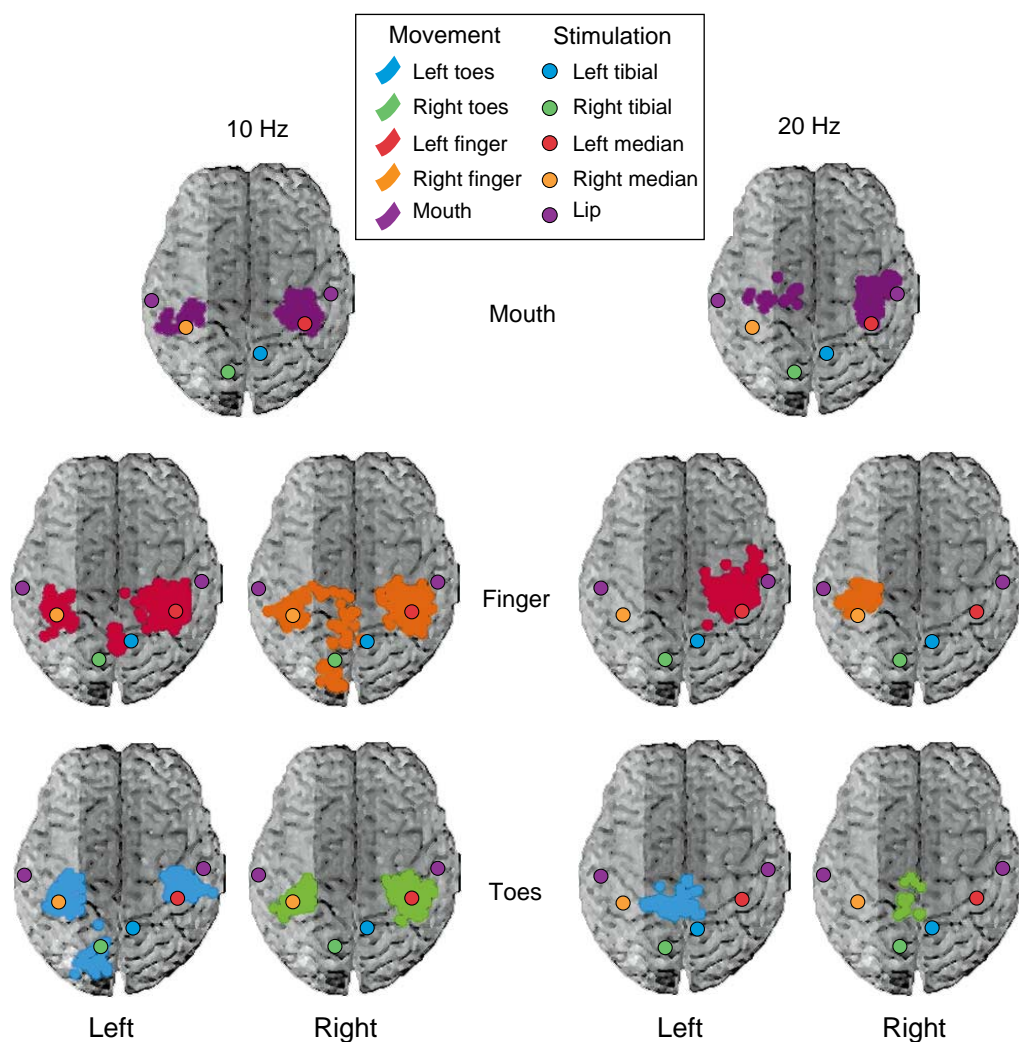
### Hemispheric balance of somatomotor reactivity

Cortical signals associated with unilateral movements imply bilateral involvement of the somato-motor cortex. The bilaterality is particularly evident in the modulation of cortical rhythms, illustrated in Fig. 5 for unimanual finger movements<sup>46</sup>. Movement-related changes in the level of spontaneous activity occurred in both hemispheres but were strongest contralaterally, particularly at frequencies above 14 Hz. The 10 Hz activity had already started to dampen 2 s before the movement. In the higher-frequency bands the suppression was relatively smaller but the movement was followed by a strong rebound of activity above the pre-movement baseline. The timecourse of the pre-movement suppression resembles the behaviour of the pre-movement slow shifts (Bereitschaftspotential, readiness field).

### Functional significance of cortical rhythms

The available hypotheses for the role of cortical macroscopic oscillations include epiphenomena, with no functional significance, and idling, which would allow the system to start more rapidly than by cold start<sup>47</sup>. In agreement with the latter interpretation, the parieto-occipital and rolandic rhythms are strongest when the modality-specific sensory input (or motor output) is minimal or monotonous. In the visual system this happens when the eyes are closed or when one looks at a homogeneous scene for a long time, and occurs in the somatosensory and motor systems when the limbs are at rest. Strong transient increases, 'rebounds', in the abundance of cortical rhythms typically occur immediately after suppression, for example after a long visual stimulus or after a voluntary movement.

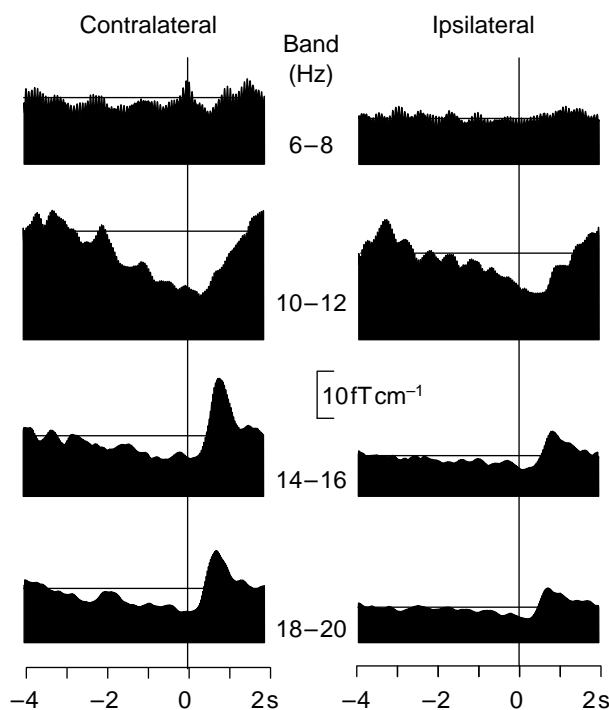
Recent data suggest that cortical rhythms might also have a role in the co-ordination of neural activity between the central and peripheral nervous systems. For example, Conway *et al.*<sup>48</sup> found a close coupling between 13–35 Hz rhythmic MEG signals from the motor cortex and the (rectified) electromyogram from the interosseus muscle during sustained contraction. They related the finding to the previously observed<sup>49</sup> synchronization of motor units in the hand muscles at frequencies of 16–32 Hz and hypothesized involvement of cortical neurones in the generation of motor-unit synchronization. Along similar lines, 8–10 Hz discontinuities of slow finger movements have been suggested previously to be due to rhythmic descending control of the motoneurone pool through corticospinal neurones<sup>50</sup>.



**Fig. 4.** Somatotopic order of sources of the somatomotor 20 Hz  $\mu$  rhythm. Source clusters for the reactive 10 Hz and 20 Hz rhythms in one subject, determined during mouth, finger and toe movements, superposed on a surface rendition of the subject's magnetic resonance images. The circles show functional landmarks obtained by stimulating electrically the same body parts and by identifying the sources of the elicited fields. Modified from Ref. 44.

Salenius *et al.*<sup>51</sup> recently found an increase in the level of the 40 Hz rolandic MEG activity during and after slow index finger movements in a subject with unusually prominent 40 Hz EEG activity. The reactive 40 Hz rhythm originated in the motor cortex and showed tight phase-coupling to the electromyographic signal from the moving muscle, with a time difference of 20 ms. It thus seems evident that somato-motor cortical rhythms might, in some conditions, control the timing of the spinal motoneurone pool; the frequency range of optimal control appears highly individual. A recent MEG study on parkinsonian patients reported a strong coherence, at the frequency of resting tremor, between oscillatory activity in pre-motor and somatomotor cortices and muscle activity<sup>52</sup>. Influence of periodic activity of the peripheral sensor or effector organs, or both, on central rhythmicity has also been observed in the visual system: some of the synchronized gamma-band oscillations in cat lateral geniculate nucleus seem to reflect retinal oscillations directly (independently of the visual input)<sup>53</sup>.

Periodic input to a cortical cell can modulate properties of the cell membrane so that, functionally, the cell increases and decreases in length, in phase with the driving rhythm<sup>54</sup>. In other words, the effectiveness of dendritic synapses in modifying the output of the



**Fig. 5. Bilateral modification of somatomotor rhythms in association with unilateral finger movements.** The subject made brisk abductions of the right index finger once every 6 s and the movement-related changes in the somatomotor rhythms of both hemispheres were quantified by means of temporal spectral evolution (TSE) analysis (see Fig. 2) in narrow frequency bands. The vertical lines illustrate the onset of movement. Modified from Ref. 46.

cell might vary in a phase-locked manner with the rhythmic background activity. Cortical rhythms could thus be associated with periodic facilitation of impulse transfer and synaptic strengths, phenomena potentially useful for refinement of synaptic connections during development and learning. Indeed, the coherent 25–35 Hz oscillations in the sensorimotor cortex of awake behaving monkeys have been suggested to facilitate interactions between neurones during exploratory and manipulative movements<sup>55</sup>. In a similar way, the observed rhythmic modulation in the human somatomotor cortex could promote temporal association of different neuronal populations into functional units controlling accurate limb movements.

The higher-frequency (40–80 Hz) cortical oscillations have been proposed repeatedly to have a role in feature binding and object segmentation<sup>56</sup>. McCulloch<sup>57</sup> hypothesized, 50 years ago, that the alpha rhythm continuously scans cortex to discover excited areas. Llinás<sup>58</sup> later advocated a similar role for 40 Hz oscillations, assuming that the 40 Hz rhythms originate in thalamus and then project to various cortical regions. Temporal variations of magnetic-field patterns were considered to indicate that a rapid scanning of the brain takes place from front to back, and forms the basis for 'unitary perceptual entities', constructed from the multitude of details of the perceived world. The experimental evidence for this fascinating hypothesis is still controversial.

### Concluding remarks

A surprisingly small number of synchronized cells might determine the recorded macroscopic signal that reflects the gross activity of a cell population<sup>26</sup>. Macroscopic cortical rhythms therefore probably arise

in areas with the most synchronous signal transfer. It is worth emphasizing that changes in the synchronization of a neuronal population can occur without significant changes in the mean neuronal firing rates, and thus without changes of blood flow and metabolism. This means that modulation of neuronal synchrony, although potentially of high importance for local information processing, might remain undetected in positron emission tomography and functional magnetic resonance imaging.

In basic neuroscience, studies of brain rhythms are experiencing a renaissance after decades of neglect. Although animal experiments continue to be the main source of information about the significance and neural basis of cortical oscillations<sup>59</sup>, brain rhythms of conscious human beings are gaining increasing interest. With the new whole-scalp neuromagnetometers, the reactivity and dynamics of these rhythms can now be studied non-invasively and more accurately than previously, under a multitude of experimental conditions.

Many previous experiments studying relationships between behavioral states and brain rhythms need re-interpretation when more information accumulates about the sites of origin and generation mechanisms of the rhythmic signals. Studies of cortical rhythms and their modulation by tasks and external stimuli has opened a promising route to further understanding of the function of the human brain. Is Hans Berger's dream of brain rhythms unveiling the neural basis of psychic phenomena finally becoming true?

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## BOOK REVIEWS

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### Zoophysiology: Nervous System Regeneration in the Invertebrates

by Stacia B. Moffett, Springer-Verlag, 1996. DM198.00 (xi + 208 pages) ISBN 3 540 59454 X

This monograph is an excellent and long-overdue summary of cell-body and axonal regeneration of neurons in many invertebrate phyla (Cnidaria, Ctenophora, Platyhelminthes, Nemertea, Nematoda, Annelida, Arthropoda and Mollusca). The monograph provides a rather nice balance between an encyclopedic description of regenerative capabilities in different phyla (Chapter 2) and general descriptions of important processes in nerve regeneration (Chapter 3: 'Early responses to neuronal injury', Chapter 4: 'Pathfinding by the growth cone' and Chapter 5: 'Synapse formation and alteration during regeneration').

This monograph is particularly valuable for several reasons. First, it introduces research scientists and clinicians to neuronal regenerative processes common in invertebrates that are present, but not common, in vertebrates (especially mammals); for example, the regeneration of nerve cell bodies, the survival for weeks to years of axonal segments severed from their cell bodies, and the high specificity of regenerated connections. Second, it provides an overview of regenerative processes that are common to both invertebrates and vertebrates; for example, changes in excitability following axotomy, sealing of cut axonal ends, morphology and

physiology of growth cones, and pathfinding by growth cones. Third, it provides readers with a bibliography that lists most of the important papers in this somewhat-ignored field. From these papers, in turn, interested readers can access all the research literature of invertebrate neuronal regeneration. Finally, this monograph is exceedingly valuable because it demonstrates clearly why mechanisms of neuronal regeneration are often more easily addressed in invertebrates whose simpler nervous systems have identifiable neurons. The principles learned from these invertebrate systems have proven applicable to mammals and have provided insights to the repair of human neurons.

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### Primer on the Autonomic Nervous System

edited by David Robertson, Phillip A. Low and Ronald J. Polinsky, Academic Press, 1996.  
HB £59.00; PB £29.00 (xv + 343 pages) ISBN HB 0 12 589760 X; PB 0 12 589761 8

When King George III confronted the historian Gibbon, who had just completed yet another book, he remarked 'Scribble, scribble, scribble, eh Mr Gibbon? Another fat book, eh, Mr Gibbon?'. What right do authors and book editors have to add continuously to the already gigantic piles of published books, most of them destined to pass into oblivion without seeing an

update or revision? Might these be attempts by editors and authors to barge into libraries without first asking permission to enter? But publishers do not put out books just for fun: their acquisition editors seek new topics and willing editors or authors because they recognize a new niche in the market, and a new opportunity for profit.

The autonomic nervous system (ANS) has only just become a marketable commodity. Twenty years ago it was the province of anatomists, pharmacologists, physiologists, and other basic scientists who did not see patients and could not contribute to the coffers of medical schools. The clinical examination of the nervous system as it was then taught to students, and even residents in neurology, did not include the ANS. Dysfunction of the ANS was deemed so rare that it was not considered a useful preoccupation for practicing doctors; its disorders (when they were even recognized) were treated