

**REVIEW**

RECENT non-invasive human studies show that rhythmic oscillatory activity of the motor cortex and the primary motor units or muscle are coherent during isometric contraction, with peak frequencies around 20 Hz or 40 Hz, depending on the contraction strength. The cortical signals precede the motor unit firing and appear to reflect modulation of the common central drive to the spinal motoneurons. The rhythmic modulation may form as tool for efficient driving of motor units but we express some reservations about the assumed binding and attention-related roles of the coherence. It is of interest for understanding of cortical control of voluntary movements and the pathophysiology of various motor disorders, as well as for unravelling the functional significance of cortical rhythms. *NeuroReport* 10:1-12, © 1999 Lippincott Williams & Wilkins.

**Key words:** Attention; Binding; Coherence; Corticomotor-neuronal fibers; Human; Magnetoencephalography; Motor cortex; Motor unit; Synchrony

**Rhythmical corticomotor communication**

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**Introduction**

The brain controls muscles by sending complex and accurate spatiotemporal firing patterns to the spinal motoneuron pools. It has been known since the early 1930s that the human rolandic (sensory-motor) cortex displays a rhythmic activity, and the rhythmic discharges in the electromyograms (EMGs) of human contracting muscles have been well established since the beginning of this century. Although the similarities of hand tremor and human scalp electroencephalogram frequencies [1], as well as the rhythmic modulation of descending motor commands [2], were emphasized already 60 years ago, the central and peripheral research lines have only recently converged when coherence between human cortical and muscular signals was demonstrated both during isometric contraction and slow movements [3,4]. This review gives a brief summary of motor cortex-muscle coherence studies. We start by describing human electroencephalographic (EEG) and magnetoencephalographic (MEG) sensorimotor rhythms and the corresponding signals in monkey cortex. We then briefly review motor unit synchrony found in electromyographic (EMG) recordings and finally concentrate on the MEG-EMG coherence and its possible functional significance.

**Cortical sensorimotor rhythms**

*Human studies:* Several regions of the healthy human cortex display their own intrinsic rhythms, the

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**NeuroReport**

of the primary motor cortex. For example, exploratory finger movements abolish the rebound totally [15], implying activation of the motor cortex. Even imagery of finger movements or mere viewing of another person making the movements suppresses the rebound [16,17].

*Monkey studies:* Recordings of sensorimotor rhythms in monkeys have largely confirmed the human  $\mu$  rhythm data, showing more prominent oscillations during rest than movement. Recent studies have concentrated on movement-related oscillations. Murthy and Fetz [18-20] observed that local field potential (LFP) oscillations, as well as single and multi-unit activity, in monkey sensorimotor cortex were more frequent during exploratory hand and arm movements that involved sensorimotor coordination than during repetitive movements. Interestingly, cycle-triggered EMG averages suggested that the oscillations had an effect on corticospinal neurons which influence muscle activity. The oscillations were distributed over relatively large cortical areas, which was considered to imply synchrony of coactivated regions.

Staes and Dehaene [21] also observed oscillatory (15-50 Hz) LFPs in monkey motor cortex during skilled voluntary movements. These oscillations were synchronous over more than 7 mm across primary motor and premotor cortices, and they occurred predominantly before the visual stimulus which cued initiation of a movement and ended before movement onset, although they occasionally continued into the initial phases. In a subsequent study [22] fast oscillations were associated with movements during untrained reaching but not during simple repetitive movements.

**Motor unit synchronization**

*Functional motor neuron pools:* The primary motor cortex is essential for skilled hand and finger movements. One of its major influences on the spinal cord is via the corticospinal tract, including some direct corticomotoneuronal (CM) connections. The CMs branch considerably at the spinal level and some CMs facilitate several functionally synergistic muscles while they often simultaneously inhibit the antagonists [23]. The functioning of the motor unit (MU; the spinal motoneuron and all muscle fibres it innervates) is controlled in a complex way by influences from both CMs and other descending fibres as well as interneurons.

One central question of motor coordination is how the MUs and muscles are grouped during different movements. Motoneurons form 'pools' which, in combination, produce the multitude of

most dominant ones peaking around 10, 20, and 40 Hz with modality- and frequency-specific reactivity to different tasks and manipulations. The human rolandic  $\mu$  rhythm consists of  $\sim$ 10 and  $\sim$ 20 Hz components, which differ in their generation sites, timing and reactivity. It has been noted that many authors make a distinction between  $\sim$ 10 Hz and  $\sim$ 20 Hz  $\mu$  rhythm, given the characteristic comb shape of the rolandic rhythm, we consider it more proper to call the whole rhythm  $\mu$  according to the original definition by Gastaut [9]. In intraoperative recordings, Jasper and Penfield [10] observed strictly localized  $\sim$ 25 Hz activity in the motor cortex, and MEG data similarly suggest that the  $\sim$ 20 Hz component of the  $\mu$  rhythm is generated more anteriorly than the  $\sim$ 10 Hz rhythm in the rolandic region, probably reflecting its main contribution from the primary motor cortex [6,7].

The  $\mu$  rhythm is primarily ipsilaterally, but with contralateral dominance, in association with movements [7-13]. During longer to shorter contractions, the rhythm reappears [10]. Both the 10- and 20 Hz levels of the  $\mu$  rhythm increase within 1 s after a voluntary movement, or after electric stimulation of a peripheral nerve [6,7,14]. The post-movement  $\sim$ 20 Hz rebound follows in a somatotopic manner the moving body part (hand, foot, mouth) whereas the  $\sim$ 10 Hz activity tends to cluster close to the hand region [7]. Because a major part of the  $\sim$ 20 Hz MEG activity seems to arise from the motor cortex, the  $\sim$ 20 Hz rebound after peripheral nerve stimulation is a useful tool for probing the functional state

of movements that can be realized by means of a limited number of muscles. The CM recruitment is flexible and selective so that, for example, a CM cell and its target muscle can be dissociated depending on the task.

*Short-term synchronization:* In motor physiology, oscillatory firing of MUs is well established. MUs fire asynchronously under normal conditions but they can also fire in synchrony. In short-term synchronization the MUs fire within a few milliseconds from each other. The abundance of synchrony detected in surface EMG depends on the number of MUs in the whole population and on the proportion of the synchronously firing MUs. As in any system with simultaneously active synchronous and asynchronous elements, the synchronous ones dominate the signal.

During isometric contraction, MUs of the same muscle tend to fire in synchrony more often than expected by chance [24-26]. The synchrony, well reflected in cross-correlograms, has been attributed to branched-axon input to spinal motoneurons which is likely to include supraspinal influences: MU synchronization can be altered voluntarily, for example using auditory feedback triggered by coincident MU firing [27]. Furthermore, reduction or loss of fine motor control after nervous lesions is associated with decreased MU synchronization [28], probably because of functional disconnection of the spinal and the supraspinal levels.

MU synchronization can also occur between different muscles [29,30]. In children with cerebral palsy and marked mirror movements, MUs of homologous left and right hand muscles may be synchronous [31]. In normal subjects, synchrony has been observed between the left and right maxillaries, but not between homologous upper limb muscles that may be voluntarily co-activated but often act independently [32]. MU synchronization may also reflect task-related changes in motor commands to functionally related muscles [33-35].

*Oscillatory MU synchronization:* Synchrony between MUs does not require oscillatory behavior. However, MUs often display a common range of firing rates, and the surface EMG, reflecting the average activity of a population of MUs, may show rhythmic components. Significant coherence has been observed between MUs in the 1-12 and 16-32 Hz ranges, suggesting a common rhythmic input. For the higher frequency range the input was proposed to be of central origin [26], in agreement with the concept of common central drive [36], implying that motoneurons of the same pool receive

**MEG-EMG coherence**

the same central input. However, even under the influence of the common drive, the muscular activation is determined by the intrinsic properties of the elements involved, so that the firing patterns differ depending on the thresholds and susceptibilities of the MUs to excitation. Naturally, the modulation frequency of the central drive may differ from the firing frequencies of individual motor units.

**Human MEG-EMG coherence**

*Power and frequency:* In the first published human MEG-EMG coherence analysis, Conway *et al.* [33] found a close coupling between the 13-35 Hz rhythmic MEG signals and the (rectified) surface electromyogram from the first dorsal interosseus (FDI) muscle during weak isometric contraction. They related the finding to the previously observed synchronization of hand muscle MUs at frequencies of 16-32 Hz [26] and proposed involvement of cortical neurons in the generation of MU synchronization.

Salenius and co-workers [4] observed, in an independent study, increased level of the  $\sim$ 40 Hz rolandic MEG activity during preparation and execution of slow index finger movements in a subject who previously had been shown to display an unusually prominent 40 Hz EEG activity [37]. The reactive 40 Hz rhythm showed tight phase coupling to the EMG signal and it seemed to originate in the primary motor cortex.

More recently, Salenius *et al.* [38] confirmed the original findings of Conway *et al.* [33] about the 15-33 Hz cortex-muscle coherence during weak isometric contraction; the whole-scalp sensor array also allowed accurate source localization of the signals obtained with contraction of different muscles (see below). Figure 1A shows EMG and MEG signals during isometric contraction of an intrinsic foot muscle, both signals showing a rhythmic pattern in the same frequency range but their waveforms clearly differ. The coherence spectra in Fig. 1B illustrate significant coherence peaks at frequencies around 20 Hz for both hand and foot muscles.

These early coherence studies suggested that MU firing is modulated by a rhythmic cortical outflow. Very similar conclusions could have been made by McLachlan and Leung [39] who recorded with subdural electrodes movement-associated 32 Hz and 16 Hz rolandic rhythms from a patient with tonic postural seizures and observed a clear correlation between the cortical and EMG signals; however the latter was postulated to be a central subcortical, possibly thalamic, pacemaker driving both the cortical rhythm and the EMG activity.

During weak to moderate isometric contractions the MEG-EMG coherence does not illustrate at all frequencies which are dominant in the EMG; for example, the coherence is weak for the 10 Hz frequency which is clearly seen in the EMG spectra at weak and intermediate contractions. Similarly, McAuley and co-workers [45] emphasized the peripheral contributions to the 10 Hz MEG peaks.

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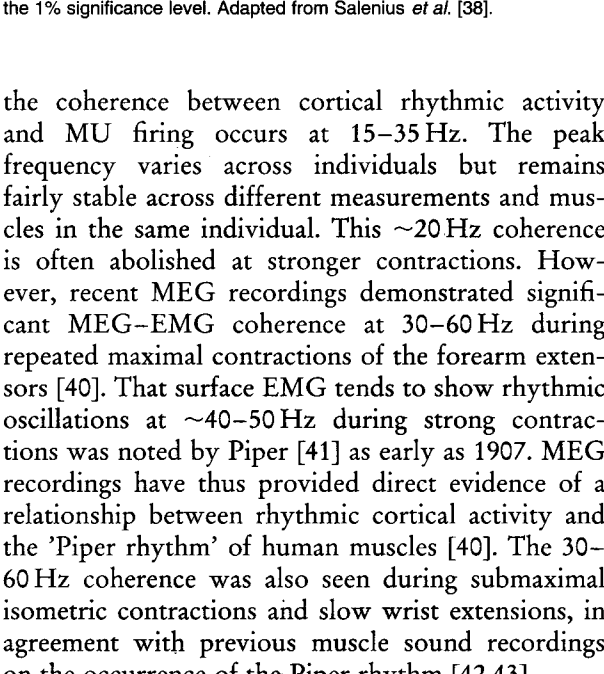


FIG. 1. (A) EMG from the right flexor hallucis brevis muscle during isometric contraction and the simultaneously measured MEG signal over the right foot area (B). Coherence spectra between MEG and rectified EMG for isometric contraction of left and right interossei (hand) and flexor hallucis brevis (foot) muscles. The horizontal dashed lines indicate the 1% significance level. Adapted from Salenius *et al.* [38].

the coherence between cortical rhythmic activity and MU firing occurs at 15-35 Hz. The peak frequency varies across individuals but remains fairly stable across different movements and muscles in the same individual. This  $\sim$ 20 Hz coherence is often abolished at stronger contractions. However, recent MEG recordings demonstrated significant MEG-EMG coherence at 30-60 Hz during repeated maximal contractions of the forearm extensors [40].

Thus surface EMG records do show rhythmic oscillations at  $\sim$ 40-50 Hz during strong contractions was noted by Piper [41] as early as 1907. MEG recordings have thus provided direct evidence of a relationship between rhythmic cortical activity and the 'Piper rhythm' of human muscles [40]. The 30-60 Hz coherence was also seen during submaximal isometric contractions and slow wrist extensions, in agreement with previous muscle sound recordings on the occurrence of the Piper rhythm [42,43].

Contraction force of a muscle may be increased either by recruiting more MUs or by increasing the firing frequency of single MUs. Typically the MU firing frequency increases with increasing force, so that the rhythm for levels of contraction, where the highest firing rates are  $\sim$ 10-40 Hz. The maximum firing frequencies vary across muscles, as does the relationship between the firing rate of CM

**R2 Vol 10 No 2 5 February 1999**

**MEG-EMG coherence**

the same central input. However, even under the influence of the common drive, the muscular activation is determined by the intrinsic properties of the elements involved, so that the firing patterns differ depending on the thresholds and susceptibilities of the MUs to excitation. Naturally, the modulation frequency of the central drive may differ from the firing frequencies of individual motor units.

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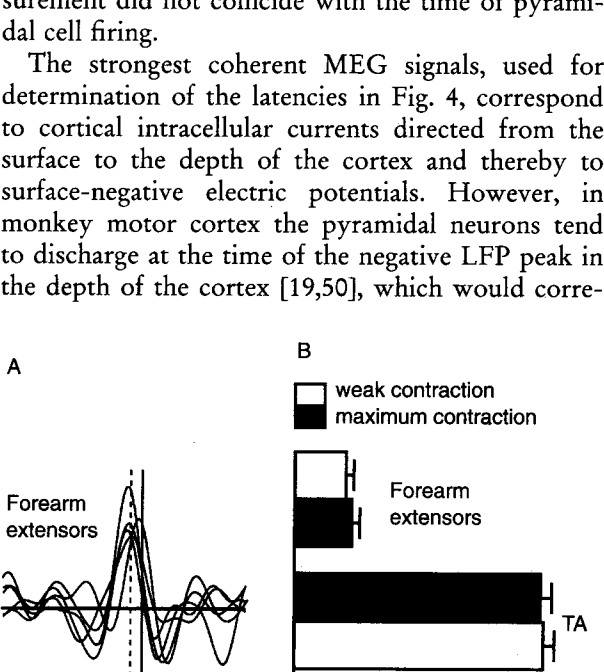


FIG. 2. Coherence spectra between MEG and the rectified EMG of right hand and foot muscles for two subjects. (A) Weak and strong contraction strengths; (B) 20-40% of maximum voluntary contraction force (MVC); (C) medium intensity of MVC and maximum-MVC. The coherence spectra are averaged over 100 trials. The EMG power spectra are arbitrarily scaled to facilitate comparison with the coherence curves. Adapted from Salenius *et al.* [38].

**R4 Vol 10 No 2 5 February 1999**

**MEG-EMG coherence**

neurons and the muscular force [36,44]. In general, the excitation frequency, required for maximum force, is proportional to the muscle contraction speed: the faster the muscle, the higher is the tetanic fusion frequency [44].

Although the MEG data show an increase in the coherent frequency with increasing force, the coherence appears to occur in discrete steps, for example from  $\sim$ 25 to  $\sim$ 45 Hz rather than in a gradual manner such as the increase of the MU frequency; it is to be noted that the main peaks of the surface EMG also display discrete jumps, as shown in Fig. 2. Thus the cortical rhythm is unlikely to drive individual MUs, but it rather modulates the firing of a population of MUs, and the increase in dominant coherent frequency with contraction strength is, at least in part, decoupled from the increase in MU firing rate. Figure 2 also illustrates that the MEG-EMG coherence does not occur at all frequencies which are dominant in the EMG; for example, there is no coherence at the 10 Hz frequency which is clearly seen in the EMG spectra at weak and intermediate contractions. Similarly, McAuley and co-workers [45] emphasized the peripheral contributions to the 10 Hz MEG peaks.

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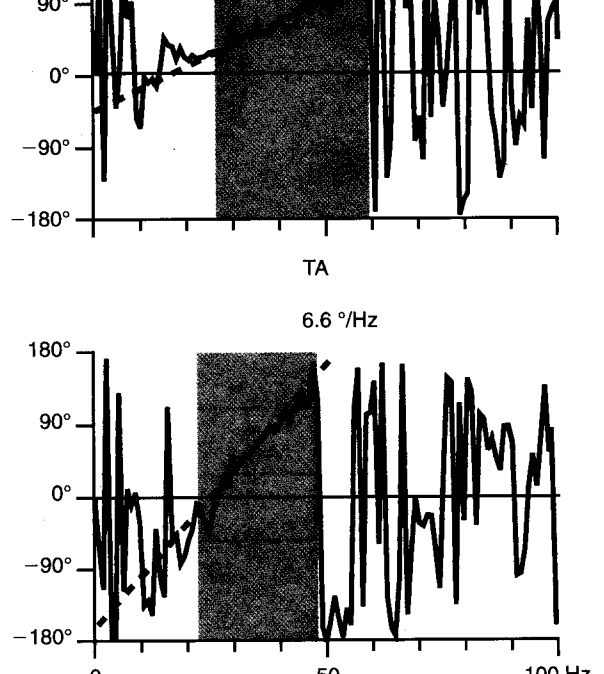


FIG. 3. (A) Spatial distributions of the strongest peaks of the MEG-EMG coherence spectra for weak contraction of the first dorsal interosseus (FDI) muscle of the right and left foot (RF and LF). The head is viewed from above. (B) MEG-EMG cross-correlograms for weak and maximum contraction of the right and left interossei (hand) and flexor hallucis brevis (foot) muscles. The EMG power spectra are arbitrarily scaled to facilitate comparison with the coherence curves. Adapted from Salenius *et al.* [38].

Recent non-invasive recordings from the monkey motor cortex showed significant  $\sim$ 20 Hz coherence between EMG and LFPs of the contralateral motor cortex during the hold phase of a precision grip task [50]. The coherence was strongest close to cortical sites where stimulation easily evoked motor responses, and significant phase-locking was also confirmed between firing of identified pyramidal tract neurons and oscillatory LFPs [51].

In the subdural recordings of McLachlan and Leung [39], the 32 Hz rhythm which was coherent with EMG activity was strongest over the postcentral and not precentral gyrus. However, such a potential maximum could well reflect activity in the

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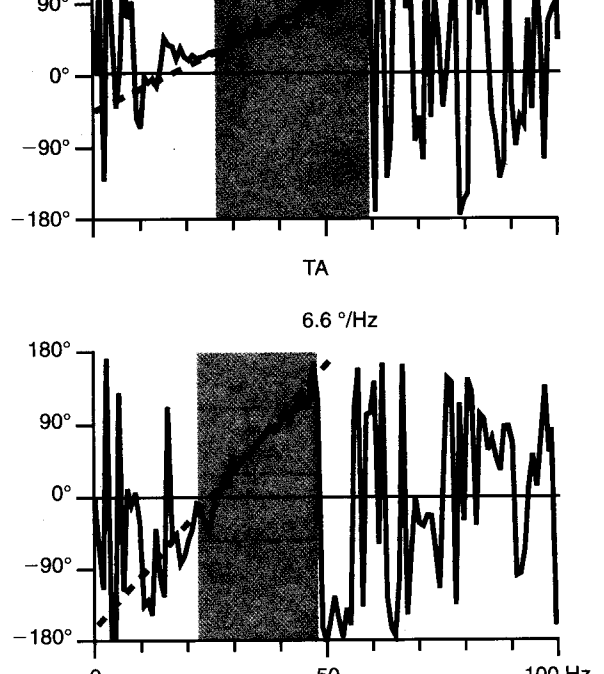


FIG. 4. Phase spectra between an MEG oscillation above the contralateral sensorimotor cortex and rectified EMG from the right forearm extensors (top), and right tibialis anterior (bottom) in Subject 1. The EMG-EMG phase (right) indicates the frequency range with significant coherence peaks. Adapted from Salenius *et al.* [38].

pend to surface positivity [53]. Thus the physiologically 'meaningful' MEG signal for time lag measurements would be the peak (of opposite polarity) just preceding the strongest cross-correlogram peak, which would add 15-25 ms to the absolute latencies and make them consistent with cortico-muscular conduction. In fact, Salenius *et al.* [38] used deflections of this orientation for their latency measurements. This choice would also be supported by studies in patients with myoclonus epilepsy: back averaging of jerk-triggered signals results in surface positivity in EEG [54] and backwards directed current dipoles in MEG [55], with about 20 ms time lags between the cortex and the muscle [56].

Although the observed time lags in fast conducting fibers, the lags between proximal and distal muscles appear too long in MEG-EMG [38], EEG-EMG [56] and EMG-EMG [57] studies, compared with the known conduction times determined by electric stimulation at the brachial plexus or magnetic stimulation at the cortex. This discrepancy is puzzling at present and needs further studies before a reliable interpretation is possible. The timing issues are feeding the spinal level by the multiple cortical sites furthering the complex level: in addition to the primary motor cortex, the premotor cortex, including the SMA, may contribute to the central outflow to the spinal motoneurons.

Halliday *et al.* [57] reported in their EEG-EMG coherence study that would indicate that the frequency/EMG delay depends on the frequency and that it would not be meaningful to derive our single frequency-independent delay. However, our results show that the delay, measured e.g. from the strongest cross-correlogram peak, is the same during weak and maximal contraction (separately for both foot and hand muscles) although the coherent frequencies differ significantly. Furthermore, and as already noted, the phase spectra show lead signals-to-noise ratio, the phase spectra show lead signals-to-noise ratio, the phase spectra show lead signals-to-noise ratio, the phase spectra show lead signals-to-noise ratio.

An alternative to the straightforward conduction delay interpretation of the relation between cortex and muscle is that the coherence is due to feedback from the muscles to influence the cortical oscillatory activity. However, the effect of spindle afference to

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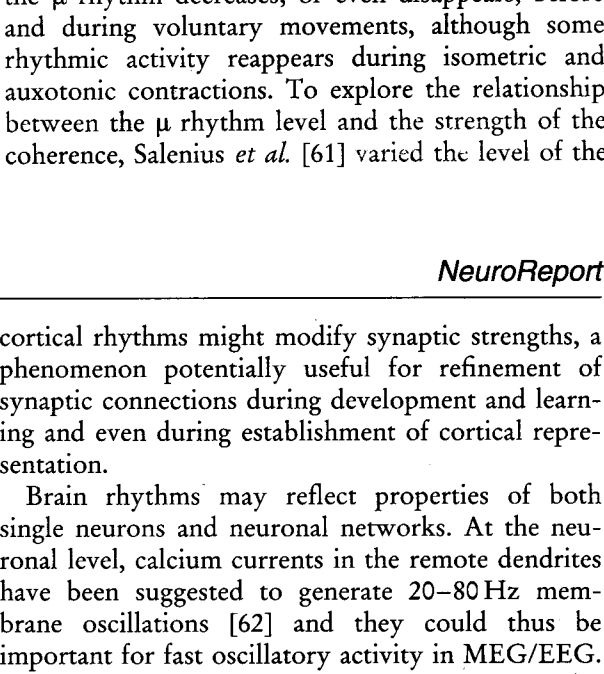


FIG. 5. MEG-EMG cross-correlograms for weak and maximum contraction of forearm extensors for five subjects. The dashed vertical line indicates the mean time lag between the EMG and MEG signals. Adapted from Salenius *et al.* [38].

**R6 Vol 10 No 2 5 February 1999**

**MEG-EMG coherence**

$\mu$  rhythm by the delivering occasional median nerve stimulation, to elicit the post-movement  $\sim$ 20 Hz rebound, while the subject was keeping steady isometric contraction in the FDI muscle.

Figure 6 shows that the time courses of the strengths of the MEG-EMG coherence and the level of the corresponding rolandic 15-35 Hz rhythm were highly similar [61], consistent with the hypothesis that the observed MEG-EMG coherence results from a rhythmic modulation of the output from primary motor cortex. In line with this result, the rhythmic changes of monkey pyramidal tract neuron firing parallel the strength of the rhythmic activity in the motor cortex [51].

Despite the clearly stronger  $\sim$ 10 Hz than  $\sim$ 20 Hz  $\mu$  rhythm component during isometric contraction, most latencies in the efference drive are dominated almost entirely by the  $\sim$ 20 Hz oscillations, demonstrating a striking disconnection between the coherent 20 Hz and the noncoherent  $\sim$ 10 Hz rhythms. Evidently the  $\sim$ 10 Hz cortical activity does not significantly influence muscular activity [50]. These findings add further support to the postulated distinction between the functional significances of the  $\sim$ 10 and  $\sim$ 20 Hz  $\mu$  rhythm components [6,8].

**Functional significance of coherent corticomotor oscillations**

The possible functional significance of cortical oscillatory activity is under continuous debate and a multitude of hypotheses have been presented. For sensorimotor rhythms the hypotheses vary from epiphenomena or idling to motor binding, i.e. integration and coordination of the activity of neuronal populations across the motor cortex, resulting in fine tuned patterns of descending commands and well coordinated movements. Of course motor cortical rhythms may have functional significance and yet the observed cortex-muscle coherence could turn out to be an epiphenomenon. For example,

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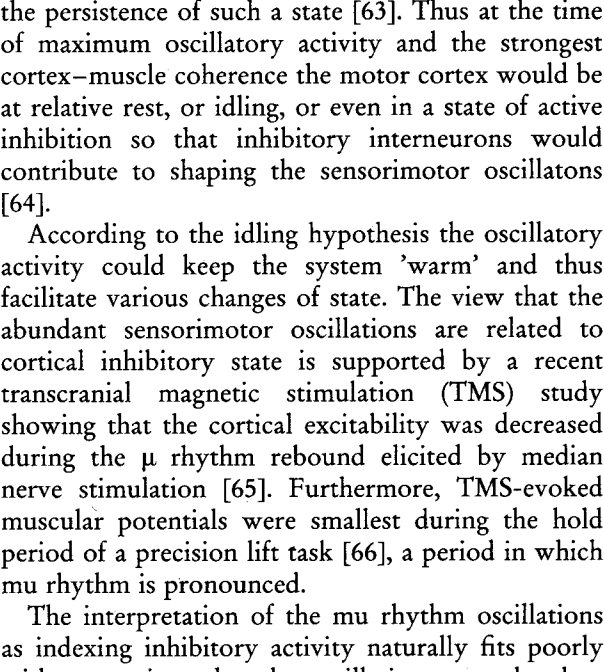


FIG. 6. Temporal behavior of MEG power (15-25 Hz; black line) and MEG-EMG coherence (15-25 Hz; white line) during isometric contraction (vertical dashed lines; interstimulus interval 3 s) for weak stimulation of the left first dorsal interosseus muscle. The curves represent averages of 1000 epochs. The MEG power curves are arbitrarily scaled to facilitate comparison with the coherence curves. Data based on Salenius *et al.* [61].

**R8 Vol 10 No 2 5 February 1999**

**MEG-EMG coherence**

an effectively of driving MUs, while maintaining as low a corticospinal firing rate as possible [46,50]. Theoretical studies show that a synchronous input produces more output firing than an asynchronous one [76,77]. Thus a group of synchronous CM neurons could be more effective in recruiting and driving MUs than a group of asynchronous CMs with the same average firing rates. Moreover, increased conductances due to continuous synaptic input during strong contraction will decrease membrane resistance and thereby shorten the membrane time constant. Thus one possibility of preferring higher modulation rates at higher contraction levels would be to link the sensorimotor guiding loop which collects sensory data necessary for monitoring effects of training and rehabilitation, as well as of reorganization after stroke and other brain lesions affecting the motor pathways. Other neurogenic and myogenic disorders may be explored as well.

The Piper rhythm seems to be lost in the muscles of untreated Parkinsonian patients [43], suggesting its dependence on normal pallidum input to the motor cortex, and during strong contraction the patients' EMG activity is dominated by a 10 Hz rhythmically which probably is suboptimal for fast and powerful contractions. Further studies of the cortical control of the hand  $\mu$  rhythm might provide new insights into the pathophysiology of Parkinson's disease.

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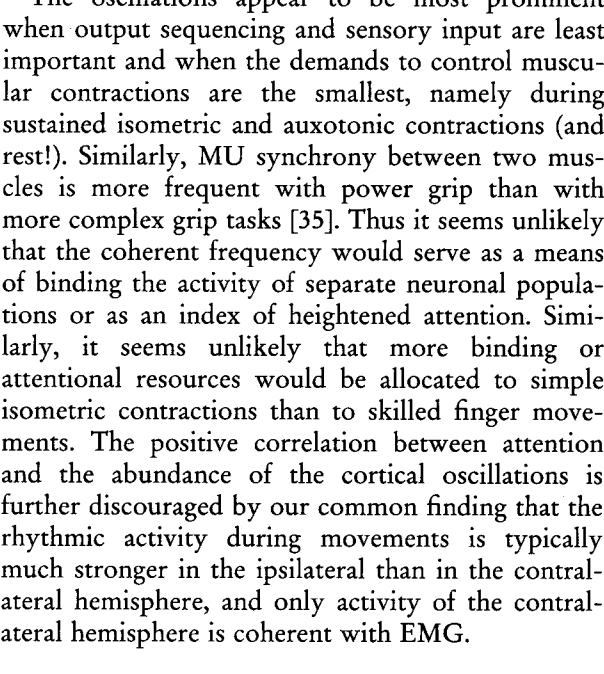


FIG. 7. Phase spectra between an MEG oscillation above the contralateral sensorimotor cortex and rectified EMG from the right forearm extensors (top), and right tibialis anterior (bottom) in Subject 1. The EMG-EMG phase (right) indicates the frequency range with significant coherence peaks. Adapted from Salenius *et al.* [38].

inaction and idling [22]. Thus despite the very close relationship between the 20 Hz oscillations and the cortex-muscle coherence, implied by their parallel occurrence, there could in principle exist separate  $\sim$ 20 Hz rhythms with different functional characteristics [6,8-70].

*Temporal reference frame, binding, and attention:* Rhythmic firing may influence membrane properties [71] and thereby facilitate synchronization of firing patterns across neuronal populations. Accordingly, the coherent 25-35 Hz oscillations in the sensorimotor cortex of awake behaving monkeys have been suggested to synchronize neuronal firing across the central sulcus, i.e. between somatosensory and motor neurons during exploratory and manipulative movements [18]. Cortical oscillations have also been proposed to be linked to a sensorimotor guiding loop which collects sensory data necessary for monitoring effects of training and rehabilitation, as well as of reorganization after stroke and other brain lesions affecting the motor pathways. Other neurogenic and myogenic disorders may be explored as well.

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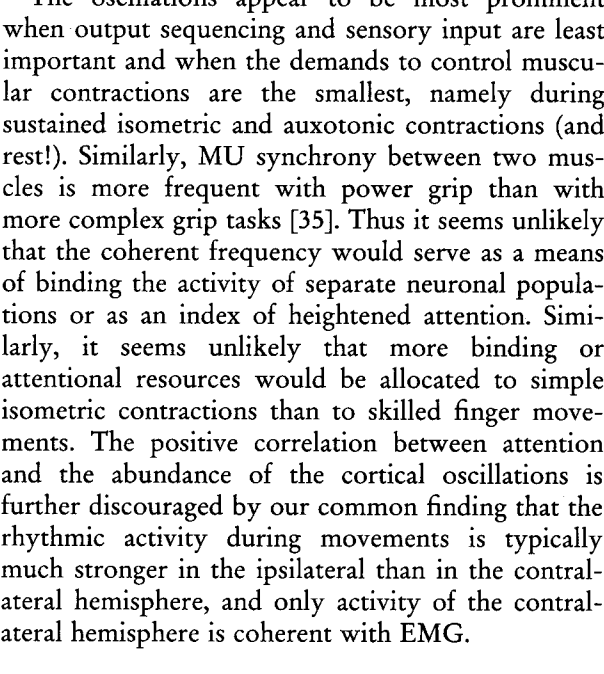


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the Piper rhythm was convincingly ruled out by Hagbarth *et al.* [60], who recorded activity from single nerve afferents of several muscles with variable spindle contents. McAuley *et al.* [45] found neither low anaesthesia, which significantly modifies peripheral nerve conduction, nor electrical stimulation increases feedback delays, altered 10, 20 and 40 Hz oscillatory EMG, tremor and muscle vibration responses. Neither did varying contraction strengths, associated with differing firing frequencies of motor units, gradually shift the observed frequency peaks. Thus the peripheral feedback seems negligible in the control of the oscillation frequency of the sensorimotor cortical rhythms.

*Coherence vs  $\mu$  rhythm level:* It is well known that the  $\mu$  rhythm decreases, or even disappears, before and during voluntary movements, although such rhythmic activity reappears during isometric and automatic contractions. To explore the relationship between the  $\mu$  rhythm level and the strength of the coherence, Salenius *et al.* [61] varied the level of the

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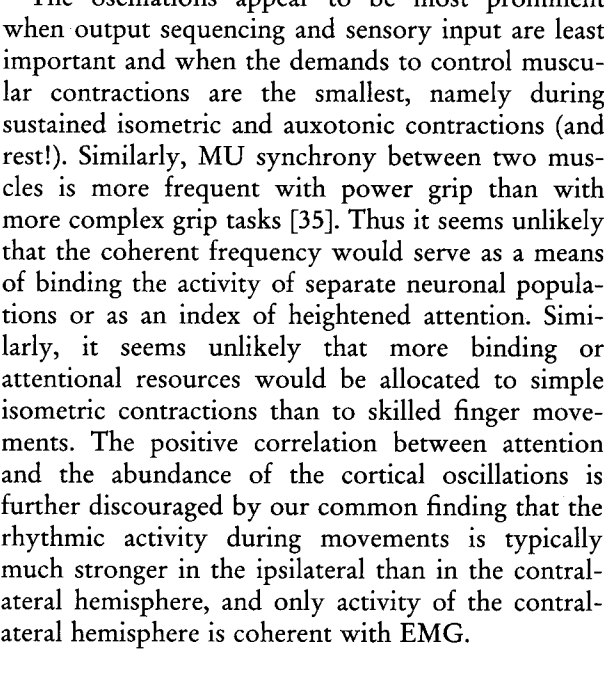


FIG. 9. MEG-EMG cross-correlograms for weak and maximum contraction of forearm extensors for five subjects. The dashed vertical line indicates the mean time lag between the EMG and MEG signals. Adapted from Salenius *et al.* [38].

cortical rhythms might modify synaptic strengths, a phenomenon potentially useful for refining motor synaptic connections during development and learning and even during establishment of cortical representation.

Brain rhythms may reflect properties of both single neurons and neuronal networks. At the neuronal level, calcium currents in the remote dendrites have been suggested to generate 20-80 Hz membrane oscillations [62] and they could thus be important for fast oscillatory activity in MEG/EEG. One reason for the different Piper frequencies for foot and hand cortices might be the larger size of the pyramidal cells in the foot than the hand motor cortex. Another possibility would be that the difference in cortical oscillation frequencies is determined by network rather than neuronal intrinsic properties.

*Idling and inhibition:* Generally, the amplitudes of  $\sim$ 10 and  $\sim$ 20 Hz sensorimotor rhythms are diminished before and during movements [8,11], and often even by motor imagery in the absence of movement [10