

Synaptic interactions mediating synchrony and oscillations in primate sensorimotor cortex

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Abstract – The appearance of oscillatory modes of ‘gamma’ activity in many cortical areas of different species has generated interest in understanding their underlying mechanisms and possible functions. This paper reviews evidence from studies on primate motor cortex showing that oscillatory activity entrains many neurons during periods of exploratory manipulative behavior. These oscillatory episodes synchronize widely spread neurons in sensorimotor cortex bilaterally, including descending corticospinal neurons, as evidenced by correlated modulations in EMG activity. The resulting neural synchronization involves task-related and -unrelated neurons similarly, suggesting that it is more likely to play some global role in attention than mediating any obvious interactions involved in coordinating movements. Intracellular recordings have elucidated the strength and types of synaptic interactions between motor cortical neurons that are involved in both normal and oscillatory activity. Spike-triggered averages (STAs) of intracellular membrane potentials have revealed serial connections in the form of unitary excitatory and inhibitory post-synaptic potentials (EPSPs and IPSPs). More commonly, STAs showed large synchronous excitatory or inhibitory potentials (ASEPs and ASIPs) beginning before the trigger spike and composed of multiple unitary events. ASEPs involved synchronous activity in a larger and more widespread group of presynaptic neurons than ASIPs. During oscillatory episodes synchronized excitatory and inhibitory synaptic potentials occurred in varying proportions. EPSPs evoked by stimulating neighboring cortical sites during the depolarizing phase of spontaneous oscillations showed evidence of transient potentiation. These observations are consistent with several functional hypotheses, but fit best with a possible role in attention or arousal. © 2000 Elsevier Science Ltd. Published by Éditions scientifiques et médicales Elsevier SAS

synchrony / oscillations / spike-triggered average / gamma activity / synaptic potentials

1. Introduction

In awake behaving monkeys, sensorimotor cortex neurons display two modes of activity. The predominant mode consists of modulated firing rates, related in relatively reliable ways to specific sensory or motor events. More intermittently, under appropriate behavioral conditions cells can also exhibit transient oscillatory activity in the ‘gamma’ frequency range of 20–40 Hz [3, 10, 17, 19–21, 25]. Cortical gamma activity has been documented extensively in different cortical areas in many species [1, 4, 5, 13, 15, 16, 22, 24, 26, 29–31], generating considerable interest in its possible function. The most robust measure of oscillatory activity in primate sensorimotor cortex is the local field potential (LFP); many neurons show a tendency to fire in the negative phase of the LFP oscillations. These two modes of activity are further distinguished by their cortical distribution: the locations of cells with particular types of task-re-

lated modulation are somatotopically organized, but the oscillations can occur in phase over wide cortical territories, including pre- and postcentral cortex and both hemispheres. During these coherent oscillations many units at these diverse sites become transiently synchronized. We have investigated the relation of these oscillations and their coherence to behavior in macaque monkeys [19–21]. Intracellular recordings in awake monkeys have elucidated the synaptic interactions underlying both regular firing and oscillatory activity [6–8, 18].

2. Materials and methods

We recorded LFP and unit activity in sensorimotor cortex of three monkeys performing exploratory hand movements to retrieve raisins from the slots of a Klüver board or from unseen locations (the hand of the experimenter, held to the side of the head, which was fixed) [20]. The monkeys also performed alternating wrist movements in a step-tracking task. Cortical activity was

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recorded with movable tungsten microelectrodes and multiple fixed implanted electrodes. To identify oscillatory cycles, the LFP signal was passed through a time-amplitude window discriminator to generate trigger pulses for clear cycles between 10 and 40 Hz. These pulses were used to calculate cycle-triggered averages of LFPs and rectified EMG activity, as well as cycle-triggered histograms of unit activity.

A second set of experiments on synaptic interactions involved recording the intracellular (IC) membrane potentials of motor cortical neurons and simultaneously recording extracellular (EC) spikes of neighboring neurons [18] and LFPs [6, 7]. Recordings were made in lightly anesthetized monkeys and in awake monkeys performing alternating wrist movements in a target tracking task. To investigate synaptic interactions between cortical neurons, pulses from the EC spikes were used to compute spike-triggered averages (STAs) of IC potentials. The STAs accepted only sweeps in which no IC action potentials occurred, to eliminate possible confounding contributions from such action potentials.

3. Results and discussion

3.1. Behavioral correlates of oscillations

Gamma frequency oscillations were documented in LFP and unit activity in sensorimotor cortex of three monkeys performing trained wrist movements and untrained exploratory arm and hand movements [20]. The mean frequency of LFP oscillations was about 26 Hz, and the number of cycles per episode was variable, with a mean of 4.2. Neither the frequency nor the number of cycles per episode varied significantly with the observed behavior. However, oscillatory episodes occurred more often during free exploratory limb movement, as the monkeys retrieved raisins from a Klüver board ($0.6 \text{ episodes} \cdot \text{s}^{-1}$) or from unseen locations ($0.6 \text{ episodes} \cdot \text{s}^{-1}$); they occurred less often during performance of repetitive wrist flexion and extension movements with the hand constrained in a manipulandum ($0.2 \text{ episodes} \cdot \text{s}^{-1}$) and while the monkey sat quietly at rest ($0.2 \text{ episodes} \cdot \text{s}^{-1}$). Robust oscillations were also evoked by presentation of arousing stimuli, such as the sight of a capture glove. During free arm movement the occurrence of oscillatory episodes had no reliable relation to movements or to bursts of agonist muscle activity. *Figure 1* shows records

of the field potentials and EMG of contralateral forearm muscles as the monkey began exploratory movements. The LFP power in the 20–40 Hz band increased in both pre- and postcentral sites, but showed no clear relation to EMG bursts.

3.2. Cortical extent of coherent oscillation

LFPs were recorded simultaneously at multiple sites in the sensorimotor cortex during the above behaviors. Cross-correlation of LFPs at different sites indicated that oscillations could become synchronized at widely separated sites. The strength of inter-site LFP correlation was measured from sliding-window cross-correlograms in two ways: by the probability of occurrence of significant correlations (relative to time-shifted controls) and by the average amplitude of the significant correlation. Both measures of correlation strength between paired precentral sites tended to decrease with increasing horizontal separation, although the phase shift between LFP oscillations did not change significantly with separation up to at least 14 mm. Oscillations at pre- and postcentral cortical sites could also become synchronized with negligible phase shifts ($0.5 \pm 1.6 \text{ ms}$). The probability of significant correlations between pre- and postcentral LFPs increased by about 40% during exploratory behaviors relative to rest or trained wrist movements ($P < 0.01$). Recordings in left and right motor cortex revealed that LFP oscillations also occurred synchronously in both hemispheres. Moreover, these episodes entrained descending corticospinal neurons, as revealed by the correlated oscillatory modulation of average EMG in forearm muscles of both sides (*figure 2*) [19, 20]. Synchronous oscillations between motor cortical sites and contralateral hand muscles also occur during a maintained precision grip [3]. The coherence between motor cortex and forearm EMG has been documented in human subjects as well [9, 12, 14].

Activities of many single and multiple units in sensorimotor cortex become synchronized with LFP oscillations [3, 10, 21]. Cycle-triggered histograms (CTH) of units indicated that about two-thirds of the recorded units were modulated with cycles of LFP oscillations [21]. On average, units had the highest probability of spiking 3 ms prior to peak LFP negativity. Autocorrelograms of unit action potentials typically showed little evidence of periodic activity, reflecting the small proportion of time that activity was oscillatory. However, autocorrelograms of spikes selected during oscillatory episodes in LFPs exhibited clear periodicity.

Cross-correlation histograms (CCH) between pairs of units at separate sites compiled using all spikes (i.e. occurring both during and outside LFP oscillations) seldom revealed significant features. However, CCHs compiled with spikes occurring during oscillatory episodes (OS-CCH) had significant features in half of the 134 pairs recorded ipsilaterally. In these cases, both units also showed modulation in CTHs. The central peaks of the OS-CCHs occurred on average with zero delay (0.5 ± 13 ms).

Precentral cortex units in the left and right hemispheres could also become transiently synchronized during oscillations. Significant features in OS-CCH were detected in half of the 42 pairs of units recorded bilaterally; the correlogram peaks occurred with essentially zero delays (0.2 ± 8.0 ms). Again, global cross-correlations of unselected spikes showed negligible evidence of synchrony in these bilateral unit pairs, indicating that they became synchronized only during oscillatory episodes.

3.3. Tests of the sensorimotor 'binding' hypothesis

For paired sites in precentral cortex, the average strength of LFP correlations and the proportion of

oscillations that were significantly correlated were greater during exploratory behaviors such as retrieving raisins from the slots of a Klüver board than during periods of rest or overtrained repetitive wrist movements. LFP oscillations in the left and right motor cortex could become synchronized with time shifts close to 0 ms when the monkey performed bimanual manipulations. However, in contrast to predictions of the binding hypothesis, bilateral LFP synchronization occurred as often and was as strong during unimanual manipulations, when one arm was restrained with muscles relaxed, as during bimanual manipulations involving coordinated movements of both hands.

On the level of single units, if periodic synchronization were used to coordinate cells involved in a coherent movement one would expect task-related cells to be more likely to become synchronized. For pairs of precentral units recorded ipsilaterally, the probability of occurrence of significant features in the OS-CCH and the magnitude of correlation peak was statistically the same whether both units of the pair were task-related (33/56 pairs = 59%) or only one unit was task-related (20/39 pairs = 51%). These results suggest that many different

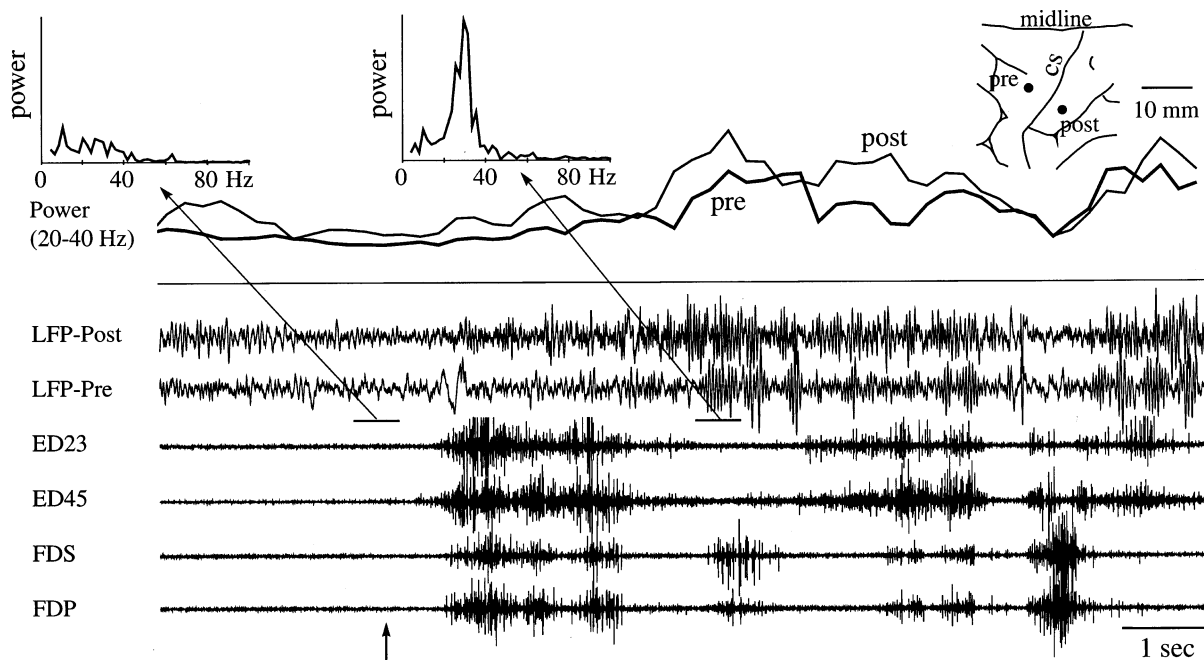


Figure 1. Increases in LFP oscillations during exploratory hand movements. Traces from bottom-up show EMG activity of forearm muscles controlling wrist and digits, LFPs recorded at pre- and postcentral sites, and LFP power in the 20–40 Hz band. Power spectra were calculated for 256-ms windows successively shifted by 100 ms. Recordings begin with monkey at rest. At the arrow a raisin was offered to the side of the head (which was fixed in space) and the monkey extracted it from the experimenter's hand. Top insets show sample power spectra from indicated intervals during rest and movement (left), and location of cortical recording sites (right) (from [21]).

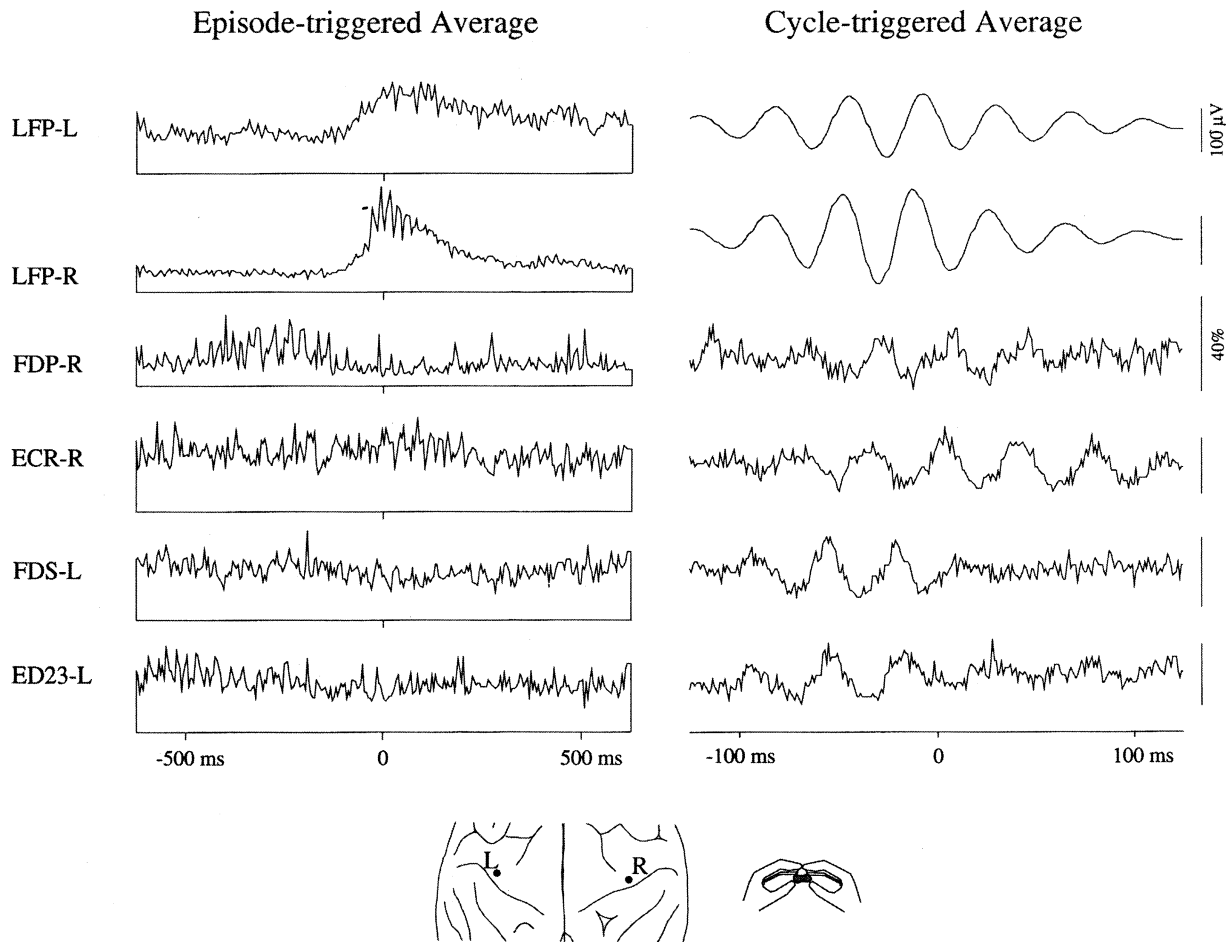


Figure 2. Relation between bilateral LFP oscillations and forelimb muscle activity in a monkey performing bimanual movements. Left records show episode-triggered averages of rectified LFPs and EMG activity of flexor and extensor forearm muscles recorded on the right (R) and left (L) sides. These averages are aligned on onset of oscillatory episodes in the right motor cortex and show concomitant LFP episodes in left motor cortex, but little evidence of episode-related increases or decreases of muscle activity. Records on right show cycle-triggered averages, aligned with cycles of LFP oscillations in right motor cortex, and show synchronized cycles in left cortex and periodic modulation of EMG on both sides. Diagram at bottom shows recording sites (from [21]).

types of cells can become transiently synchronized specifically during LFP oscillations, even if their modulated firing rates during non-oscillatory periods are associated with different movement parameters. Surprisingly, oscillations did not preferentially synchronize coactivated, task-related neurons, again suggesting that synchronous oscillations are not required to mediate sensorimotor association or binding.

However, non-oscillatory synchrony between units – as evidenced by a single central peak in their cross-correlogram (without secondary peaks) – still could play a role in mediating such associations. A previous study cross-correlated the activity of neighboring task-related motor cortex

neurons and found that such synchrony peaks were relatively independent of the similarity in their firing patterns [11, 27]. The possibility remains that non-oscillatory synchrony may reflect a binding mechanism that is superimposed on task-related modulations. Of course, the coordination of neural activity involved in a given movement must be mediated by synaptic interactions, which would generate some synchrony between connected cells. Distinguishing the synchrony produced by normal synaptic interactions of coactivated cells from synchrony specifically related to coding gestalt relationships represents a formidable experimental challenge.

3.4. Intracellular measures of synaptic interactions between cortical neurons

To investigate directly the mechanisms of synaptic interactions between cortical neurons in other experiments, we obtained simultaneous recordings of intracellular (IC) membrane potentials and extracellular (EC) spikes of neighboring neurons [18], and LFPs [6, 7] in lightly anesthetized and awake monkeys. In the absence of oscillatory activity, spike-triggered averages (STAs) of IC membrane potentials revealed four basic types of spike-related potentials: unitary excitatory and inhibitory post-synaptic potentials (EPSPs and IPSPs), with onsets following the trigger spike, and synchronous synaptic potentials in the form of ‘average synchronous excitatory potentials’ (ASEPs) and ‘average synchronous inhibitory potentials’ (ASIPs), both straddling the EC triggers (figure 3). The average amplitudes of these spike-related potentials are given for cases in which the potentials appeared in isolation. The figure also tabulates the relative proportions of these events occurring among all the STAs that showed any

features. Given separately are the proportion of STAs that showed each feature alone (% pure), and the proportion in which the feature was superimposed on an ASEP (% mixed). The most commonly observed feature was the ASEP, which occurred alone in 64% of the STAs and in combination with the other potentials in another 18% of the records [18]. The fact that ASEPs occurred about ten times more often than serial EPSPs suggests that operations in cortical circuits use synchronized activity more commonly than isolated serial interactions. In about 22% of the ASEP pairs, the trigger cell also had an excitatory or inhibitory connection to the IC cell. Thus, 78% of the ASEP pairs involved synchronous firing of apparently unconnected cells.

Comparing the sizes of the synchrony potentials with the sizes of the corresponding post-synaptic potentials provides an estimate of how many unitary events underlie the synchrony events. Assuming linear summation, the amplitude ratios suggest that the ASEPs would be composed on the average of about 4.7 EPSPs, while the ASIPs consist of about 2.1 IPSPs. The ASEPs had earlier onset

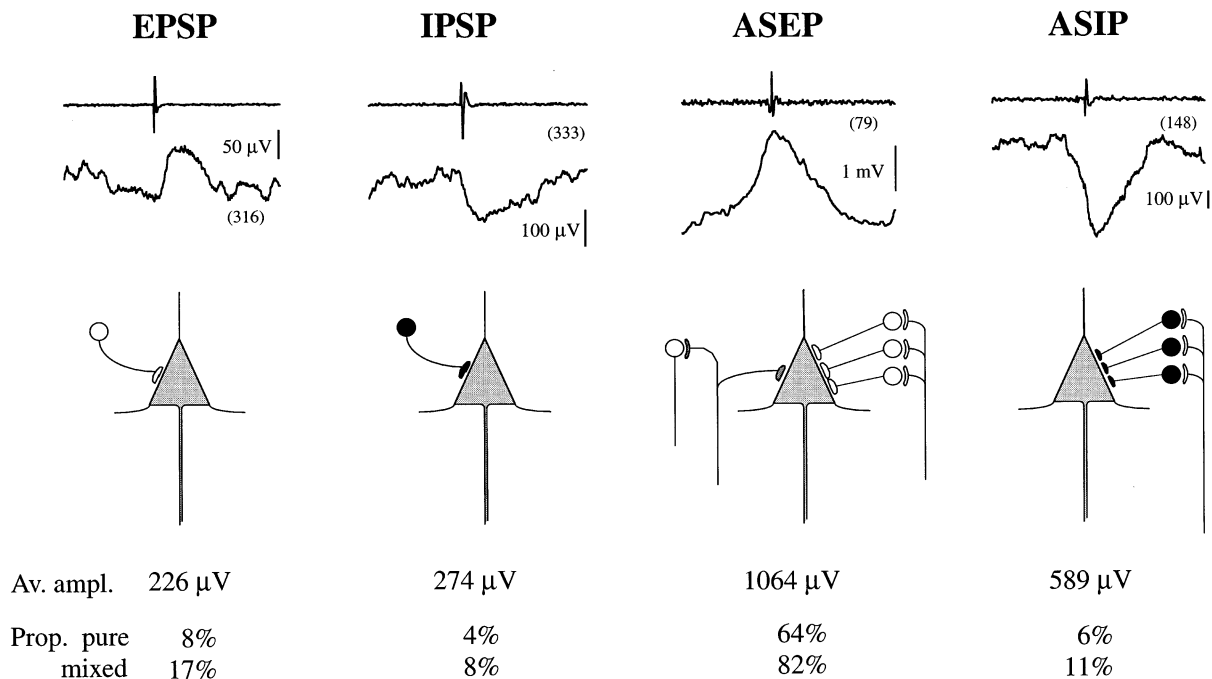


Figure 3. The four basic types of synaptic potentials revealed by STAs of cortical neurons. Examples of each type are shown at top: STAs show triggering EC spikes (upper traces) and averaged IC membrane potentials (lower traces). Possible synaptic circuits mediating these effects are diagrammed schematically below. Pyramidal-shaped units represent IC cells, and circles represent EC cells. Open boutons represent excitatory synapses, black boutons are inhibitory and shaded boutons of the common input could be either excitatory or inhibitory. Tabulated below are the average amplitudes of potentials and percentage of all feature-containing STAs that exhibited the indicated feature, either alone or in combination with ASEPs (from [18]).

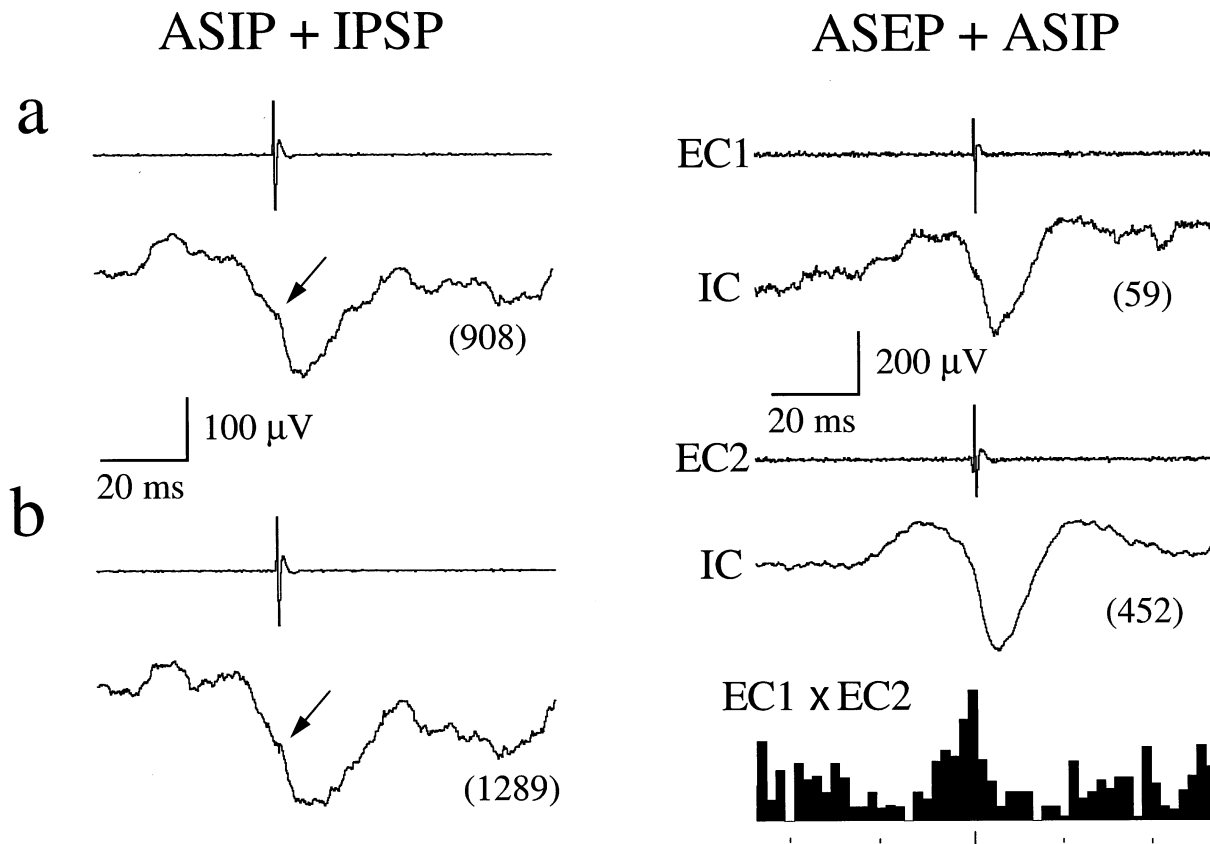


Figure 4. Combinations of synchronous and serial synaptic connections revealed in STAs. Left shows two examples of IPSP (onset at arrow) superimposed on ASIP. Right shows two examples of inhibitory potentials superimposed on ASEPs. These STAs were obtained with two simultaneously recorded EC cells and the same IC cell. The peak in the cross-correlogram of the two EC cells (bottom) reflects their synchronization (from [18]).

times (-14 ms relative to the trigger) and longer durations (18 ms) than the ASIPs (-5.5 ms onset and 11 ms duration), suggesting that the synchronized EPSPs comprising the ASEP are more dispersed temporally than the IPSPs. The pairs of neurons exhibiting ASEPs were also more dispersed spatially than the pairs showing ASIPs. Many ASIPs exhibited a post-spike notch (figure 4, left), suggesting that the trigger cell itself generated an IPSP and was part of a synchronized group of inhibitory neurons. This is shown schematically in the lower right diagram of figure 3, in which one cell of the synchronized presynaptic group is the trigger cell. This relationship was directly confirmed when two EC units producing ASIP-IPSPs in the same IC cell were recorded simultaneously: their cross-correlation histogram showed a synchrony peak (figure 4, right). Together, these observations suggest that cortical inhibition is mediated by synchronized groups of relatively lo-

calized inhibitory neurons, while synchronized excitation can involve more widely distributed connections.

3.5. Intracellular potentials associated with oscillations

The basic types of spike-related potentials described above were obtained in the absence of oscillatory activity. To investigate synaptic interactions during oscillations, CTAs of membrane potentials were aligned with cycles of the intermittent oscillatory LFPs recorded at neighboring sites. These CTAs revealed sub-threshold membrane potential oscillations with depolarizing and hyperpolarizing components, occurring with different relative proportions in different cells. The depolarizing potential during oscillations had a mean amplitude of $896 \mu\text{V}$; the hyperpolarizing component averaged $-577 \mu\text{V}$. Surprisingly, these values are

comparable to the amplitudes of the non-periodic ASEPs and ASIPs. STAs compiled selectively during oscillations usually showed larger ASEPs than did STAs compiled outside oscillations (for the same trigger cell), indicating an increased number of synchronous EPSPs during periodic oscillations. ASIPs could be larger (56%) or smaller (33%) during oscillatory LFPs. These observations indicate that both excitatory and inhibitory cortical neurons contribute in varying degrees to sustaining oscillatory activity, in agreement with observations in cat visual cortex [4, 13].

In addition to being driven by synaptic interactions, oscillatory activity also may be sustained by intrinsic mechanisms in some cortical neurons. Examination of the cells' interspike interval trajectories revealed that certain cortical cells that have a strong propensity to fire at 25–35 Hz also have a characteristic after-hyperpolarization duration of about 30 ms, a feature not present in interspike trajectories of most other neurons investigated [6, 8].

One possible consequence of synchronous oscillations may be the modulation of the strength of synaptic connections by Hebbian mechanisms. During cortical oscillations the synaptic connections that are active in phase with depolarizations could be potentiated. To investigate the possible role of oscillatory synchrony in synaptic plasticity, EPSPs were evoked by intracortical microstimuli delivered at nearby sites in phase with the oscillatory LFP cycles. By delivering stimuli at low rates between oscillatory episodes it was possible to compare the sizes of the EPSPs just before and after synchronization with the oscillatory episodes. A transient increase in EPSP amplitude was observed in all three cells in which EPSPs were evoked during the IC depolarizing phase, but not in two cells stimulated at other phases of the oscillations [6, 7]. This suggests that depolarization associated with oscillations may mediate short-term potentiation of synaptic transmission. This potentiation lasts only a brief time since the post-episode EPSPs revert to the pre-episode size during the interval between oscillations. Similar effects have been reported in *in vitro* studies of the hippocampus [23] and have been suggested to occur in thalamocortical circuits [28].

4. Conclusions: possible functions of oscillations

Observations to date indicate that robust intermittent cortical oscillations appear in sensorimotor

cortex of awake monkeys, but the data still do not resolve their functional role, if any. The observations are consistent with several hypotheses, including the possibility that oscillations are simply an epiphenomenon of excitability, performing no behavioral function. The problem with this null hypothesis is that the widespread entrainment of neural activity into synchronized bursts would be expected to interfere with normal rate coding functions. Comparing the firing rates before and during oscillatory episodes revealed that oscillations transiently increased low rates and reduced high rates, 'clamping' the overall rate during oscillations to the cells' mean firing rate [21]. This effect of oscillatory activity would not necessarily interfere with rate coding if these two modes could be readily superimposed. Such superposition appears plausible, since rate-coded information would still propagate in the appropriately interconnected network of functionally related cells, despite the intermittent global oscillatory mode of a larger network. Indeed, such superposition of evoked response and local network activity has been well documented in visual cortex [2]. Similarly, in sensorimotor cortex of epileptic patients widespread synchronized interictal electroencephalographic spikes occur in otherwise functional cortex [1]. So it seems possible for the oscillatory episodes to appear as tolerable epiphenomena in cortex without necessarily interfering with superimposed rate-coded activity mediating normal functions.

Nevertheless, it is tempting to consider whether the brain has learned to put such a robust phenomenon to some functional use. Since synchronous activity can be propagated more effectively than asynchronous activity, synchrony has been suggested to be an effective mechanism for binding neurons into ensembles representing gestalt relationships [26]. Moreover, oscillatory synchrony would have an advantage of effectively recruiting neurons more widely than aperiodic synchrony [15]. In primate sensorimotor cortex, cells involved in a given behavior may share some common synchronous drive, as evidenced by central peaks in the cross-correlograms of neighboring task-related neurons. However, this form of task-related synchrony usually does not show periodic oscillations [11, 27]. Several different circumstances have been reported to favor the occurrence of oscillatory activity in primate sensorimotor cortex. Synchronous oscillations have been reported to occur during an instructed delay period prior to movement and to disappear during the overt movement [10]. In apparent contradiction, oscilla-

tions have been observed to appear during a maintained precision grip, where their function could be understood in terms of the enhanced efficacy of a synchronized rhythm in activating motoneurons [3]. In our studies oscillatory episodes occurred more often during exploratory hand movements, but without any consistent relation to bursts of EMG (figures 1, 2). These oscillations entrained task-related and -unrelated neurons equally and oscillatory coherence between sites did not depend on their relation to the task, indicating that under these movement conditions coherent oscillations do not seem to be performing any obvious sensorimotor binding function [20, 21].

A second functional hypothesis that may resolve the apparent discrepancies proposes that oscillations could be related to an increased level of attention. Periodic oscillations may play a functional role in behavioral arousal [24] or the increased perceptual attention involved in exploratory movements [20]. At the cellular level one such role could be a global potentiation of synaptic interactions. This may involve relatively transient potentiation of connections between networks of neurons beyond those involved in performing the immediate task, thus facilitating wider associations. Oscillations may also mediate the long-term potentiation of connections between neurons underlying motor learning, a capacity that is typically accompanied by increased attention.

An obvious problem in resolving these different hypotheses is that they are not mutually exclusive. Indeed, several of these possible functions would overlap in many behavioral situations. The challenge for future studies is to design experimental protocols that would further resolve these possibilities.

Acknowledgements

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References

- [1] Aoki F., Fetz E.E., Shupe L., Lettich E., Ojemann G.A., Increased gamma-range activity in human sensorimotor cortex during performance of visuomotor tasks, *Clin. Neurophysiol.* 110 (1999) 524–537.
- [2] Arieli A., Sterkin A., Grinvald A., Aertsen A., Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses, *Science* 273 (1996) 1868–1871.
- [3] Baker S.N., Kilner J.M., Pinches E.M., Lemon R.N., The role of synchrony and oscillations in the motor output, *Exp. Brain Res.* 128 (1999) 109–117.
- [4] Binguier V., Fregnac Y., Baranyi A., Debanne D., Shulz D.E., Synaptic origin and stimulus dependency of neuronal oscillatory activity in the primary visual cortex of the cat, *J. Physiol. (Lond.)* 500 (1997) 751–774.
- [5] Buzsaki G., Llinas R., Singer W., Berthoz A., Christen Y. (Eds.), *Temporal Coding in the Brain*, Springer-Verlag, 1994 303 pp.
- [6] Chen D.F., Synaptic interactions between primate cortical neurons revealed by in vivo intracellular potentials, Ph.D. thesis, University of Washington, Seattle, WA, 1993, 161 pp.
- [7] Chen D.F., Fetz E.E., Effect of synchronous neural activity on synaptic transmission in primate cortex, *Soc. Neurosci. Abst.* 19 (1993) 781.
- [8] Chen D.F., Fetz E.E., Intracellular correlates of oscillatory activity of cortical neurons in awake behaving monkeys, *Soc. Neurosci. Abst.* 17 (1991) 310.
- [9] Conway B.A., Halliday D.M., Farmer S.F., Shahani U., Maas P., Weir A.I., Rosenberg J.R., Synchronization between motor cortex and spinal motoneuronal pool during the performance of a maintained motor task in man, *J. Physiol. (Lond.)* 489 (1995) 917–924.
- [10] Donoghue J.P., Sanes J.N., Hatsopoulos N.G., Gaal G., Neural discharge and local field potential oscillations in primate motor cortex during voluntary movements, *J. Neurophysiol.* 79 (1998) 159–173.
- [11] Fetz E.E., Toyama K., Smith W., Synaptic interactions between cortical neurons, in: Peters A., Jones E.G. (Eds.), *Cerebral Cortex*, vol. 9, Plenum Press, New York, 1991, pp. 1–47.
- [12] Halliday D.M., Conway B.A., Farmer S.F., Rosenberg J.R., Using electroencephalography to study functional coupling between cortical activity and electromyograms during voluntary contractions in humans, *Neurosci. Lett.* 241 (1998) 5–8.
- [13] Jagadeesh B., Gray C.M., Ferster D., Visually evoked oscillations of membrane potential in cells of cat visual cortex, *Science* 257 (1992) 552–554.
- [14] Kilner J.M., Baker S.N., Salenius S., Jousmaki V., Hari R., Lemon R.N., Task-dependent modulation of 15–30 Hz coherence between rectified EMGs from human hand and forearm muscles, *J. Physiol. (Lond.)* 516 (1999) 559–570.
- [15] Konig P., Engel A.K., Singer W., Relation between oscillatory activity and long-range synchronization in cat visual cortex, *Proc. Natl. Acad. Sci. USA* 92 (1995) 290–294.
- [16] Laurent G., Dynamical representation of odors by oscillating and evolving neural assemblies, *Trends Neurosci.* 19 (1996) 489–496.
- [17] MacKay W.A., Mendonca A.J., Field potential oscillatory bursts in parietal cortex before and during reach, *Brain Res.* 704 (1995) 167–174.
- [18] Matsumura M., Chen D., Sawaguchi T., Kubota K., Fetz E.E., Synaptic interactions between primate precentral cortex neurons revealed by spike-triggered averaging of intracellular membrane potentials in vivo, *J. Neurosci.* 16 (1996) 7757–7767.

- [19] Murthy V.N., Fetz E.E., Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys, *Proc. Natl. Acad. Sci. USA* 89 (1992) 5670–5674.
- [20] Murthy V.N., Fetz E.E., Oscillatory activity in sensorimotor cortex of awake monkeys: synchronization of local field potentials and relation to behavior, *J. Neurophysiol.* 76 (1996) 3949–3967.
- [21] Murthy V.N., Fetz E.E., Synchronization of neurons during local field potential oscillations in sensorimotor cortex of awake monkeys, *J. Neurophysiol.* 76 (1996) 3968–3982.
- [22] Pantev C., Elbert T., Lutkenhoner B., *Oscillatory Event Related Brain Dynamics*, Plenum Press, 1994.
- [23] Pavlides C., Greenstein Y.J., Grudman M., Winson J., Long-term potentiation in the dentate gyrus is induced preferentially on the positive phase of theta-rhythm, *Brain Res.* 439 (1988) 383–387.
- [24] Rougeul-Buser A., Buser P., Rhythms in the alpha band in cats and their behavioural correlates, *Int. J. Psychophysiol.* 26 (1997) 191–203.
- [25] Sanes J.N., Donoghue J.P., Oscillations in local field potentials of the primate motor cortex during voluntary movement, *Proc. Natl. Acad. Sci. USA* 90 (1993) 4470–4474.
- [26] Singer W., Putative functions of temporal correlations in neocortical processing, in: Koch C., Davis J. (Eds.), *Large Scale Neuronal Theories of the Brain*, MIT Press, 1994, pp. 201–238.
- [27] Smith W.S., Synaptic interactions between identified motor cortex neurons in the active primate, Ph.D. thesis, University of Washington, Seattle, WA, 1989.
- [28] Steriade M., Coherent oscillations and short-term plasticity in corticothalamic networks, *Trends Neurosci.* 22 (1999) 337–345.
- [29] Steriade M., Timofeev I., Durmuller N., Grenier F., Dynamic properties of corticothalamic neurons and local cortical interneurons generating fast rhythmic (30-40 Hz) spike bursts, *J. Neurophysiol.* 79 (1998) 483–490.
- [30] Traub R.D., Whittington M.A., Buhl E.H., Jefferys J.G., Faulkner H.J., On the mechanism of the gamma → beta frequency shift in neuronal oscillations induced in rat hippocampal slices by tetanic stimulation, *J. Neurosci.* 19 (1999) 1088–1105.
- [31] Wehr M., Laurent G., Odour encoding by temporal sequences of firing in oscillating neural assemblies, *Nature* 384 (1996) 162–166.