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Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys

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ABSTRACT **Synchronous 25- to 35-Hz oscillations were observed in local field potentials and unit activity in sensorimotor cortex of awake rhesus monkeys. The oscillatory episodes occurred often when the monkeys retrieved raisins from a Klüver board or from unseen locations using somatosensory feedback; they occurred less often during performance of repetitive wrist flexion and extension movements. The amplitude, duration, and frequency of oscillations were not directly related to movement parameters in behaviors studied so far. The occurrence of the oscillations was not consistently related to bursts of activity in forearm muscles, but cycle-triggered averages of electromyograms revealed synchronous modulation in flexor and extensor muscles. The phase of the oscillations changed continuously from the surface to the deeper layers of the cortex, reversing their polarity completely at depths exceeding 800 μm. The oscillations could become synchronized over a distance of 14 mm mediolaterally in precentral cortex. Coherent oscillations could also occur at pre- and postcentral sites separated by an estimated tangential intracortical distance of 20 mm. Activity of single units was commonly seen to burst in synchrony with field potential oscillations. These findings suggest that such oscillations may facilitate interactions between cells during exploratory and manipulative movements, requiring attention to sensorimotor integration.**

Oscillatory electrical events in the frequency range of 20–70 Hz have been observed in various sensory areas of the mammalian cerebral cortex (1–4). Most recently, synchronous oscillations of local field potentials (LFPs) and multiunit activity at frequencies around 40 Hz have been described in the visual cortex of anesthetized cats (3, 5) and awake monkeys (6). Such oscillations occurred coherently at widely separated visual sites within and across the two hemispheres (3, 5, 7, 8). Electroencephalogram (EEG) oscillations in the range of 20–50 Hz also occur in the motor and somatosensory cortex, especially during focused attention prior to motor acts (2, 9, 10). Pericruciate oscillations near 40 Hz occurred in cats (2), and in baboons and squirrel monkeys slower oscillations around 18 Hz were recorded at specific sites in the sensory hand areas and in area 5 (9). Scalp EEGs recorded from humans reportedly show an increase in 40-Hz signal during focused attention (10). Although the "40-Hz" oscillations are prevalent in the cortex, their function and the underlying mechanisms remain objects of speculation (11–13).

The occurrence of coherent oscillations in single or multiunit activity in response to somatosensory stimulation or specific motor acts has not been reported to date, although one study reported that somatosensory stimulation disrupted rhythmic activity in single units (14). Here, we report the occurrence and properties of synchronous 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys. Oscillations in LFPs were most prominent during the performance of motor tasks that required attention and sensorimotor integration. The activities of some units separated by distances of up to 14 mm were found to be synchronized with each other and with the LFP oscillations.

MATERIALS AND METHODS

Glass-coated tungsten microelectrodes (1–2 MΩ impedance) were used to record extracellular unit activity and LFPs from the motor and somatosensory cortex of awake monkeys. In some experiments, up to eight electrodes were inserted separately with a microdrive through parallel guide tubes separated by 2 or 4 mm. In other experiments specifically designed to record single-unit activity, a dual-electrode holder was used to manipulate two microelectrodes independently. In most experiments the signal from each electrode was led through two headstages (unity gain cathode followers) and filtered at two band-pass settings: between 10 and 100 Hz for the LFP, and between 0.3 and 3 kHz for single- and multiunit activity. In some experiments, electromyogram (EMG) activity was also recorded from forearm muscles with pairs of stranded stainless steel wires. All data were recorded on FM tape for off-line analysis.

Behavioral Training. The results were obtained with two monkeys (*Macaca mulatta*). Each monkey sat in a primate chair, which restricted bodily movements, with the head fixed during recording. A step-tracking task was performed with the entire arm fixed and the hand below the wrist inserted into a manipulandum; the monkey alternately flexed and extended its wrist in response to visual targets on a video screen (15). Other tasks involved reaching movements to the front or to the side, with the arm unrestrained below the shoulder. In a commonly used task, the monkey reached forward to retrieve raisins from the slots of a Klüver board. In another task, food pieces were offered in a box placed at the level of the monkey's hip, outside the field of vision. The monkey made tactile exploratory movements within the box to locate and retrieve the food. In a similar task, the monkey retrieved food from the experimenter's hand at unseen locations to one side of the restrained head. We also monitored periods of quiet sitting to observe spontaneous oscillatory events. To better correlate the timing of events, we recorded behavior on a video tape with simultaneous LFPs and audio clicks generated from each cycle of the oscillatory episodes.

Data Analysis. Cycle-triggered averages were compiled to document events correlated with the LFP. A time-amplitude window discriminator generated trigger pulses from each cycle of the oscillation, when the voltage (*i*) exceeded an above-noise threshold, and (*ii*) passed through a voltage window after a specified delay. These pulses were used to trigger a multichannel averager to compile cycle-triggered averages of (*i*) LFPs at all sites, (*ii*) time histograms of unit activity, and (*iii*) rectified EMG activity. Power spectra of the LFPs were calculated using a fast-Fourier transform algorithm to define the frequency of the oscillatory events.

Abbreviations: LFP, local field potential; EMG, electromyogram.
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RESULTS

Parameters of the Oscillatory LFP. Fig. 1 illustrates examples of intracortical LFP recordings from adjacent sites in the motor cortex, showing two episodes of oscillatory activity at ≈28 Hz. Such readily recognizable oscillations increased in amplitude above baseline and decreased after a variable number of cycles. Power spectra of LFPs confirmed that the power in the range of 25 to 35 Hz increased up to 10 times above the baseline power. The shape of the oscillatory bursts varied considerably; some episodes were spindle shaped, others started or ended abruptly, and some were continuously sustained for many cycles, as illustrated by the continuous record in Fig. 2*A*. The number of cycles within an episode varied from 3 cycles (the minimum required to identify an oscillation) to 30 successive cycles, with an average of ≈5 (Fig. 2*B*). The rate of occurrence of oscillatory episodes varied with behavior (see below). The frequency of the oscillations varied slightly from one episode to the next (Fig. 2*C*), with an overall mean of 27.4 ± 3.1 (SD) Hz.

Single-Unit Activity. In many experiments the activity of single or multiple units was recorded simultaneously with the field potentials. Often we could generate pulses from a single unit within a multiunit record by using a time-amplitude window discriminator. Single-unit isolation was confirmed by a repeatable action potential waveform and a refractory period in the autocorrelogram. Many units were classified according to their response to natural stimulation of the limb and their relation to active movements.

All recorded units exhibited spontaneous discharge in the absence of significant oscillations in the field potentials. When oscillations appeared in the field potentials, many units tended to fire rhythmically in phase with the LFP oscillations (Fig. 1). Autocorrelation functions of the overall unit activity seldom revealed appreciable oscillatory activity. However, autocorrelograms of unit activity compiled selectively during oscillations in the LFP often showed clear periodicity. A total of 129 units were recorded at sites that exhibited identifiable LFP oscillations. Of these units, 63 (49%) were modulated with the LFP oscillations in cycle-triggered averages. This number probably overestimates the actual proportion of units showing modulation, since oscillatory units were sometimes sought. Observations to date have not revealed any relation between the likelihood of units to synchronize with the oscillations and their tendency to respond to sensory stimulation or discharge during active movements.

Units located at depths >800 μm from the surface of the cortex tended to discharge during the negative phase of the LFP oscillations recorded at the same site. The few units that were isolated above 800 μm tended to fire during the positive phase of the LFP oscillations recorded superficially. Comparing the LFP from a movable electrode with simultaneous recordings from a reference electrode revealed that the phase of the LFP oscillations changed with depth and was completely reversed in polarity below 800 μm. This reversal of polarity within the cortex suggests an intracortical source of the LFPs in superficial layers.

Spatial Distribution of Oscillatory Sites. To document oscillations at different cortical sites, we recorded from multiple electrodes simultaneously within a circular region of ≈15 mm diameter centered over the hand area. Most often, recordings were obtained with two electrodes; in some sessions, simultaneous recordings were made from up to eight electrodes, with neighboring tracks separated by 2 mm. When the electrodes straddled the central sulcus the intracortical separation of their tips, measured tangentially along the cortex, was larger than their physical separation. The oscillations in LFPs recorded from electrodes separated by 2 mm or less were always synchronized, although the background activity in the two differed. The phase difference between the oscillations in the electrodes at similar depths (usually below 800 μm) was negligible. In the precentral gyrus, coherent oscillations occurred over distances of 14 mm in the mediolateral direction, parallel to the central sulcus (Fig. 3). The amplitudes of the oscillations did not differ significantly across this distance. However, with increasing separation, the proportion of synchronous oscillations decreased and more of the oscillations occurred independently.

In the anterior–posterior direction, synchronized oscillations occurred across the central sulcus in many instances (Fig. 4). The coherence of the oscillations observed in the raw data was confirmed by cycle-triggered averages (Fig. 4). The largest physical separation between pre- and postcentral electrode tracks that revealed synchronized LFP oscillations was 8 mm, which would correspond to an estimated tangential separation of 20 mm in the unfolded cortex. To test whether single units in the pre- and postcentral cortex became synchronized during the oscillatory episodes, we recorded simultaneously from two sites across the central sulcus in the hand area. When the monkeys retrieved raisins from small slots in a Klüver board either with or without the aid of vision, robust oscillations occurred in the precentral areas. Oscillations occurred less often in the postcentral areas, but those that did occur were synchronized with the precentral oscillations. During these oscillatory episodes, unit activity in the two sites tended to become synchronized. The oscillatory modulation of postcentral unit activity argues against the possibility that the postcentral LFP oscillations were simply recordings of precentral fields at a distance;

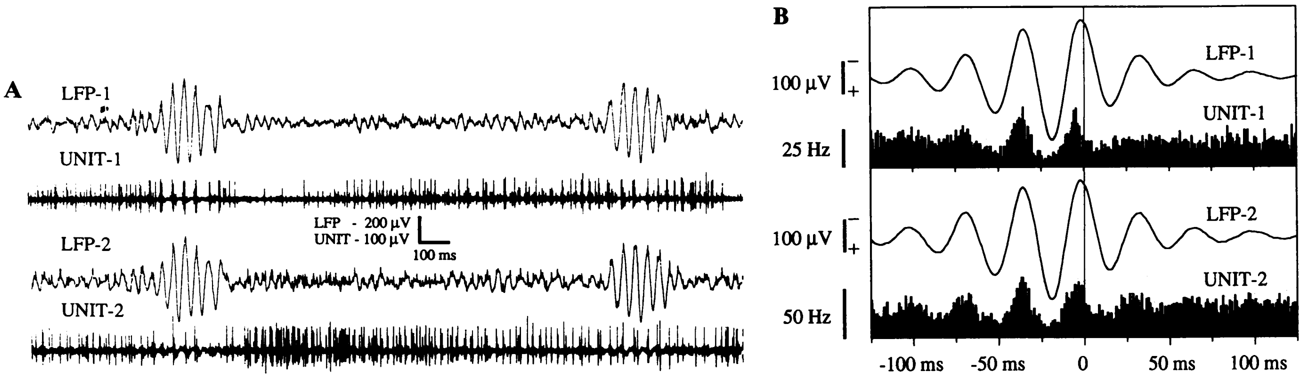

FIG. 1. (*A*) LFPs and unit activity recorded at two nearby sites in the motor cortex of a monkey retrieving a raisin from a Klüver board. Upper and lower pairs of traces show LFPs and unit activity from electrodes 1 and 2, respectively. Raw traces and averages of LFPs are shown with positivity downward for all figures. Units on both electrodes responded to passive and active flexion of digit 2. Electrodes were separated by ≈800 μm and were located at depths >800 μm. (*B*) Cycle-triggered averages of LFPs and unit activity for sites in *A*. Averages were aligned on cycles of LFP-2. LFPs were in phase with each other and units tended to discharge during the negative phase of the LFP.

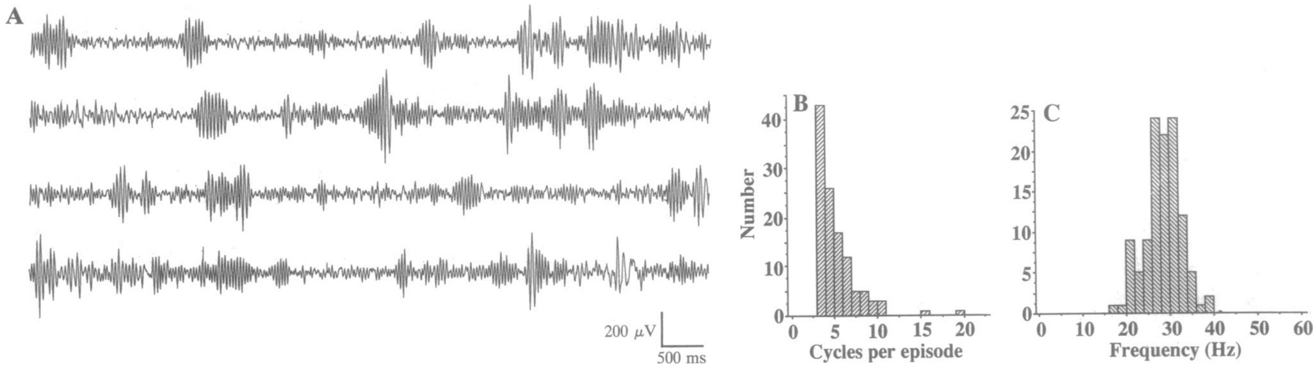

FIG. 2. (*A*) LFP from a precentral site illustrating the variety of shapes, durations, and amplitudes of oscillations. Successive lines show a continuous record made when the monkey was wresting raisins out of the experimenter's hand at the side of the monkey's head. (*B*) Distribution of the number of cycles in each oscillatory episode recorded while the monkey retrieved raisins from a Klüver board. Pulses were generated from each cycle within an oscillatory episode. At least three successive pulses with separations of <60 ms were required to identify an oscillatory episode. (*C*) Distribution of cycle frequencies of the oscillatory episodes calculated from the same data as in *B*. Frequency for each episode was calculated as the reciprocal of the average interpulse interval for successive cycles of each episode.

instead, the unit activity confirms local sources of oscillatory activity in postcentral areas.

Behavioral Correlates. The rate of occurrence of the oscillatory episodes and the durations of single episodes were calculated for different behavioral conditions. As shown in Fig. 5, the parameter of the oscillations that changed the most with behavioral condition was the rate of occurrence of oscillatory episodes. Other parameters, such as the intrinsic frequency or the maximum amplitude of the oscillations and the duration of the oscillatory episodes, did not appear to be systematically correlated with behavioral conditions.

The behavior that elicited the oscillations most robustly was exploratory arm and hand movements that required attention to sensorimotor coordination. For instance, oscillations appeared often when the monkeys retrieved raisins from an unseen container, using tactile and proprioceptive cues to explore the container. In a similar task, the monkey was offered raisins to the side of the restrained head, beyond the range of peripheral vision. The monkey had to palpate the raisin in the investigators' hand and wrest it free. In this task, oscillations appeared very reliably in the precentral areas. Retrieving raisins from slots in a Klüver board visible in front of the monkey also evoked oscillations. When raisins were simply placed in the slots of the board while the monkey's arm was restrained, oscillations also appeared for variable durations, even though movements to retrieve the raisin were precluded. Oscillations also occurred during manipulative movements that did not involve food, such as removing adhesive tape from the contralateral arm or manipulating inedible objects. When the monkey performed a routine, overtrained step-tracking task, generating ramp-and-hold flexion and extension torques about the wrist, the cortical oscillations occurred less frequently than during free arm movements (Fig. 5). The oscillations showed no consistent trial-by-trial relation to different phases of the flexion–extension task, although response averages of some sessions showed that oscillations occurred preferentially during the flexion phase. When the monkey was sitting at rest making no overt movements, a few spontaneous oscillations occurred infrequently, significantly ($P < 0.001$) less often than during all other behaviors except the flexion–extension task (Fig. 5). The cycle frequency of spontaneous oscillations (26.3 Hz) was slightly lower than the frequency of oscillations during other behaviors (27.5 Hz). It was significantly lower only when compared with the frequency when the monkey reached to the side for raisins (*t* test; $0.001 < P < 0.01$).

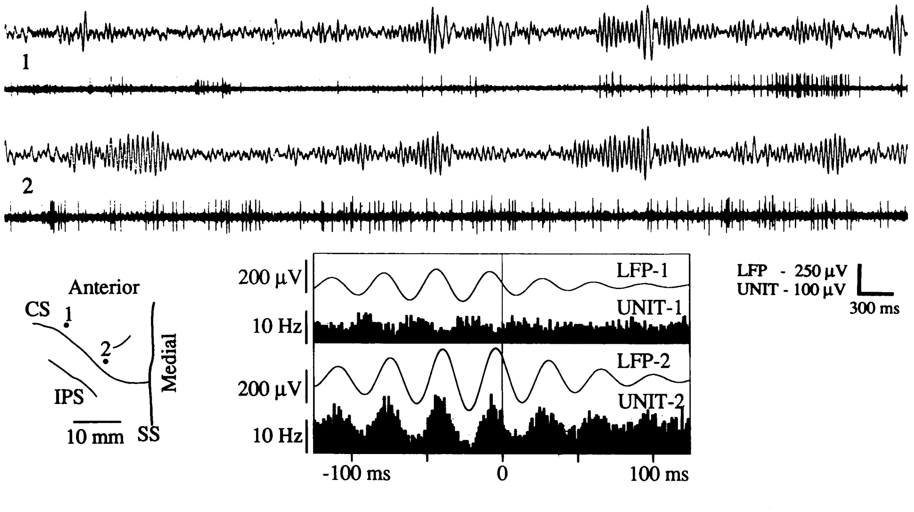

FIG. 3. (*Upper*) LFPs and unit activity from sites in the motor cortex separated by ≈14 mm. Medial electrode (*2*) corresponding to the lower two traces was situated in the proximal arm area of the motor cortex. Units at the lateral site (*1*) tended to discharge with movements of the wrist and digits. Many episodes of oscillations were synchronized in the two electrodes, but some episodes in the lower trace were not accompanied by similar events in the upper trace. (*Lower Middle*) Cycle-triggered averages of LFPs and units aligned on cycles in LFP-2. Although the units were not tightly correlated with the LFP oscillations, cycle-triggered averages revealed a tendency for the large unit at site *2* to synchronize with the LFP oscillations. (*Lower Left*) Approximate recording locations are indicated in a sketch of the cortical surface. SS, sagittal sinus; CS, central sulcus; IPS, intraparietal sulcus. (*Lower Right*) Calibration bars are for traces in *Upper*.

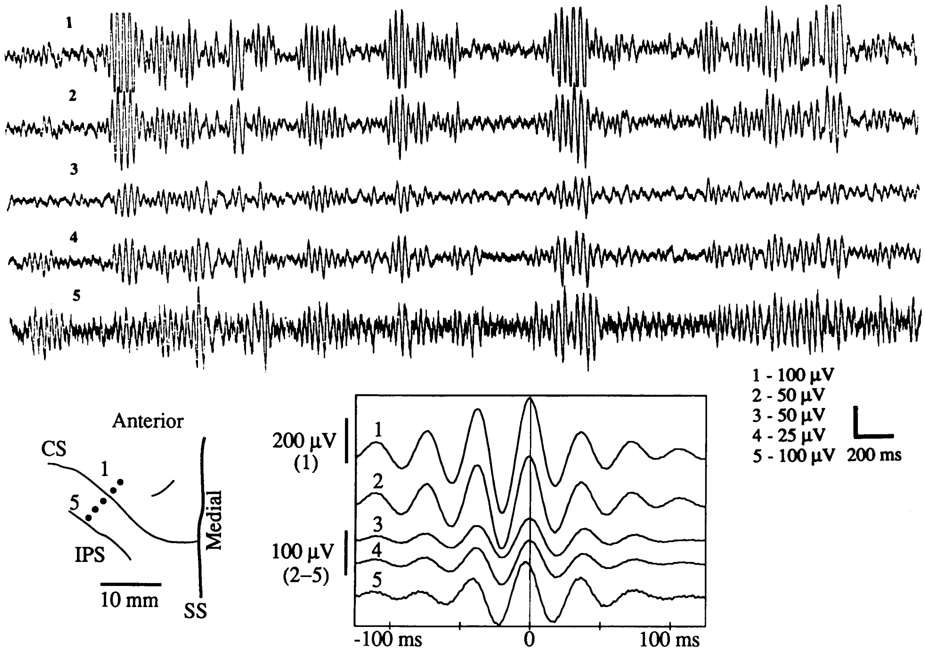

FIG. 4. (*Upper*) LFPs recorded simultaneously in five anterior–posterior tracks separated by 2 mm each. Electrode sites, marked on the sketch of the cortical surface, straddled the central sulcus. (*Lower Middle*) Averages of LFPs aligned on triggers from oscillatory cycles in LFP-1. The monkey was reaching for a raisin offered to the side of its head by the experimenter. (*Lower Left*) Sketch of cortical surface as in Fig. 3. (*Lower Right*) Calibration bars are for LFP traces in *Upper*.

To investigate the relation between oscillatory cortical activity and peripheral muscle activity, we compiled averages of rectified EMGs aligned with the onset of oscillations as well as averages of LFPs aligned with the onset of EMG bursts. These averages did not reveal any consistent relation between the timing of oscillatory episodes and bursts of EMG activity in forearm muscles (Fig. 6*A*). However, cycle-triggered averages of EMGs compiled by triggering from a particular phase of each cycle did reveal correlated oscillations in the average EMG (Fig. 6*B*). The effects appeared in both flexor and extensor muscles. This finding suggests that the cortical oscillations do have a statistical effect on corticospinal neurons, which affect muscle activity. Preliminary data suggest that the cycle-triggered EMG modulation was strongest during the raisin retrieval tasks and is negligible during the flexion–extension task.

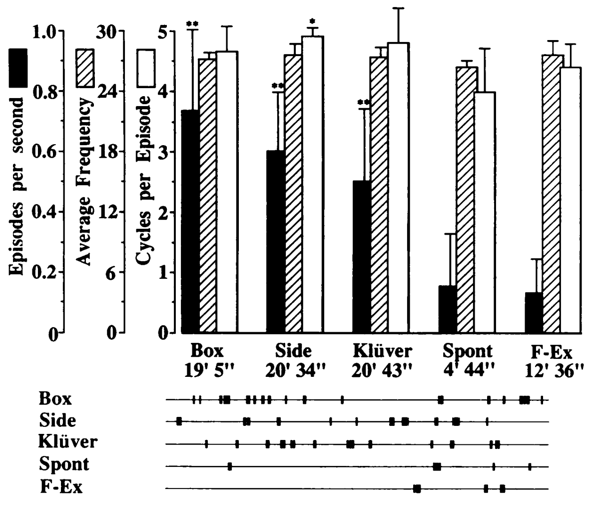

FIG. 5. Parameters of LFP oscillations as a function of behavior. Cycle frequency of the oscillations, rate of occurrence of the oscillatory episodes, and average number of cycles per episode were documented during different motor activities. Data for each behavior were pooled from many recording sessions; total time for each behavior (in minutes and seconds) is indicated below the corresponding histograms. Error bar for each histogram corresponds to 1 SD. Below the histograms, sample traces of the triggers generated from oscillations are displayed for each behavior on a continuous 20-s sweep. Behaviors are as follows: Box, retrieving raisins or pieces of apple from a box at the level of the hip, outside the range of vision; Side, retrieving raisins from the experimenter's hand at the side of the monkey's head; Klüver, retrieving raisins from slots of a Klüver board in front of the monkey; F-Ex, alternating flexion–extension of wrist; Spont, quiet sitting, no overt movement. **, Significantly different from Spont and F-Ex at $P < 0.001$; *, significantly different from Spont at $P < 0.01$.

DISCUSSION

The present results indicate that the monkey's motor and somatosensory cortex exhibits intermittent oscillatory activity at 25–35 Hz, especially while the animal performs tasks that require fine finger movements and focused attention. The oscillations were clearly identifiable in LFP recordings as well as in single- and multiunit activity. Oscillatory episodes in LFPs occurred in a variety of shapes; some were spindle shaped, while others began or stopped abruptly, suggesting that synchrony can be achieved and terminated quite rapidly. It seems significant that the oscillations occurred preferentially during demanding sensorimotor tasks, such as retrieving raisins from unseen sites, and occurred much less often during relatively "automatic" motor activity, such as overtrained alternating wrist movements. This suggests that these oscillations may play a role in attended motor behavior and sensorimotor integration. Smaller-amplitude sustained oscillations could sometimes be evoked by cutaneous stimulation of the arm, but not reliably. The oscillation frequency did not vary systematically during different behaviors tested so far, nor was the frequency correlated with other parameters such as duration of oscillatory bursts or their maximum amplitude.

These intermittent oscillations represent a mode of neural activity that clearly differs from the firing rates of units that code sensory and motor parameters. Most neurons in sensorimotor cortex discharge reliably in relation to specific somatic stimuli or particular motor responses. In contrast, the oscillations were not consistently related to movement parameters or to episodes of forearm muscle activity in the behaviors explored so far. Nevertheless, the cycle-triggered averages of EMGs suggest that they are capable of influencing cells involved in facilitating muscle activity. This is further confirmed by relatively rare spike-triggered averages of rectified EMGs that exhibited "complex features" (15), including 30-Hz periodicity (unpublished observations).

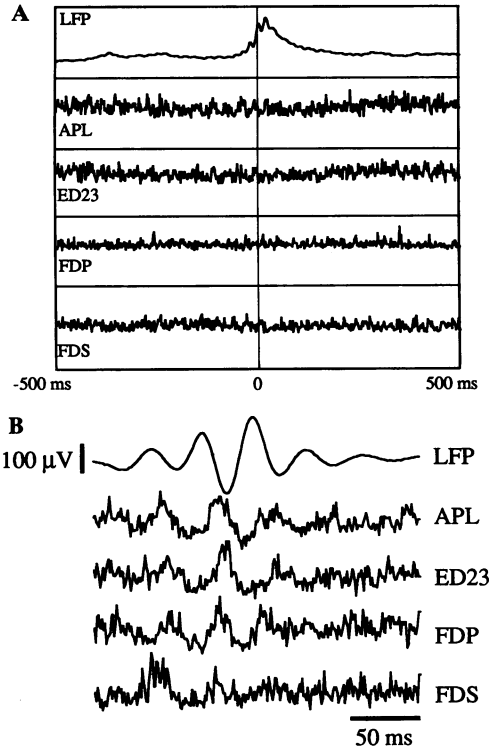

FIG. 6. (*A*) Averages of rectified LFPs and rectified EMGs from forearm muscles aligned on the onset of LFP oscillations. Monkey was retrieving raisins from the experimenter's hand. Triggers were generated from the onset of unrectified LFP oscillations. Average EMG showed no significant changes in the 1-s period straddling the onset of oscillatory episodes. Muscles: APL, abductor pollicis longus; ED23, extensor digiti II, III proprius; FDS, flexor digitorum sublimis; FDP, flexor digitorum profundus. (*B*) Cycle-triggered average of rectified EMG from forearm muscles recorded during the same period as in *A*. Average EMG of both flexors and extensors shows some modulation with LFP oscillations.

Although the oscillatory episodes were not tightly correlated with behavior, certain parameters of oscillations, such as their frequency, duration, and amplitudes have significant functional consequences. Oscillatory activity in the particular frequency range of 25–35 Hz may arise as an emergent property of the sensorimotor cortical circuitry. Oscillations of prolonged durations could be more effective in recruiting additional sites into oscillatory activity through temporal summation. Similarly, high-amplitude oscillations, if the amplitude is proportional to the number of synchronously active units, could recruit more neurons into the oscillatory mode by spatial summation. A group of neurons would be more effective in recruiting their postsynaptic targets if they discharge in synchrony than if they discharge asynchronously with the same average firing rates (16, 17).

The wide spatial distribution of coherent oscillations indicates that LFP oscillations can involve neuronal populations straddling at least 14 mm in the precentral gyrus, including the motor representation of virtually the entire arm. However, the proportion of coherent oscillations recorded at two different sites appeared to decrease with their separation. It is possible that local groups of neurons (within "columns") are synchronized during the oscillatory episodes, with different groups being synchronized at different times, as in the visual cortex (3). As the spatial separation and functional differences between these groups of neurons increase, they may exhibit less synchronized activity. In the anterior-posterior direction, synchrony also occurred across the central sulcus. The LFP oscillations had lower amplitudes at postcentral sites than in precentral regions. The precentral oscillations may have become synchronized with more localized sites in the postcentral area. We hypothesize that, during motor behaviors involving the integration of sensory cues with the motor output, functionally related sites in the sensory cortex will become synchronized with task-related sites in precentral cortex.

The polarity of the oscillations reversed completely from the cortical surface to a depth of ≈800 μm, indicating that the source of the LFP signals was in the superficial cortical layers. However, input from extrinsic structures such as the thalamus or from distant cortical sites may well contribute to generation of the oscillations. Cortical and subcortical cells are capable of generating oscillations in the 40-Hz range (18–21). The generation of oscillations in a network has also been amply demonstrated with simulations (22–24).

It has been hypothesized that coherent oscillations could be involved in feature binding in the visual system (3, 5, 13) and in pattern recognition in the olfactory system (1). Oscillations in the motor cortex are more likely to mediate some higher-order motor functions. They occur too rarely to be essential for execution or coordination of every movement. Instead, their tendency to occur preferentially during challenging sensorimotor tasks suggests that these coherent oscillations are particularly involved in neural interactions underlying attention to fine sensorimotor control.

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