SYNCHRONOUS OSCILLATIONS IN SENSORIMOTOR CORTEX OF AWAKE MONKEYS AND HUMANS

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INTRODUCTION

Oscillatory neural activity in the frequency range of 20-70 Hz has been observed in various sensory and motor cortical areas in awake and anesthetized mammals (Freeman, 1978; Eckhorn et al., 1988; Gray and Singer, 1989; Engel et al., 1991; Murthy and Fetz, 1992; Kreiter and Singer, 1992; Singer, 1993). High-frequency oscillations in the visual cortex have been suggested to play a role in associating stimulus features and in segmentation of objects in the visual scene (Eckhorn et al., 1988; Gray et al., 1989). Synchronous 20-40 Hz oscillations of local field potentials (LFP) have also been observed in the sensorimotor cortex of behaving monkeys (Rougeul et al., 1979; Murthy and Fetz, 1992; Murthy et al., 1992; Sanes and Donoghue, 1993) and humans (Sheer, 1984; Ribary et al., 1991; Pfurtscheller and Neuper, 1992). In awake, behaving monkeys, synchronous LFP oscillations were found during performance of trained motor tasks (Sanes and Donoghue, 1993) as well as during less constrained exploratory movements of the arm and hand (Murthy and Fetz, 1992). This suggests that the oscillations may play a role in attention or facilitating interactions during sensorimotor integration.

Previously, we showed that the LFP oscillations occurred more frequently during exploratory hand and arm movements that involved ongoing sensorimotor coordination, than during periods of repetitive constrained wrist movements (Murthy and Fetz, 1992). Moreover oscillations occurred synchronously over wide areas (Murthy et al., 1992), suggesting the hypothesis that the oscillations facilitate associations between cells involved in the same task. This hypothesis predicts that synchronization of LFP oscillations would tend to occur between coactivated cortical sites and be specific to particular behaviors. For instance, oscillations in pre- and

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post-central sites could become synchronized during a task that involved integration of somatosensory signals with movements. To test this hypothesis we quantitatively estimated the coherence between paired sites in pre- and post-central cortex during different behaviors. We also recorded bilaterally in the hand areas of the motor cortex when the monkey performed a manipulatory task with either hand alone and with both hands together. The associational hypothesis predicts that the LFP oscillations at the two sites would be synchronized more often during the performance of bimanual manipulations.

To determine if oscillations observed in monkeys could also occur in humans under similar behavioral conditions, we obtained subdural recordings from the sensorimotor cortex of human patients while they performed a visuomotor task. We report here the presence of clearly identifiable oscillations in electrocorticograms (ECoG) over particular sites in sensorimotor cortex which were correlated with the preparatory and execution phases of a two-dimensional tracking task. Recently, similar results were reported for electroencephalograms (Pfurtscheller and Neuper, 1992) and magnetoencephalograms (Kristeva-Feige et al., 1993).

METHODS

Two monkeys (*Macaca mulatta*) were trained to generate alternating flexion and extension torques about the wrist to track a visual target on a screen with a cursor. During this task both hands were restrained and the active hand generated isometric torque to control the cursor. The monkeys also readily performed unconstrained reaching movements to obtain pieces of food offered either to the side of their heads, in the slots of a visible Klüver board, or from an unseen box.

After the monkeys were trained, they underwent aseptic surgery in which stainless steel chambers were implanted over the sensorimotor cortical area for chronic recordings. Recordings were made from the sensorimotor cortex with two or more glass-coated tungsten microelectrodes (1-2 MΩ impedance) simultaneously while the monkeys performed the above tasks. The signal from each electrode was filtered at two band-pass settings to record LFPs (10-100 Hz) and unit activity (0.3-3 kHz). In some experiments, electromyograms (EMGs) were recorded from forearm muscles with pairs of stainless steel wires. In a few experiments behavior was recorded on videotape simultaneously with LFP traces and audio clicks generated from oscillatory cycles to correlate movements with oscillatory episodes. Data were recorded on FM tape for off-line analysis.

In collaboration with Dr. George Ojemann, epicortical recordings were made from the sensorimotor cortex of human patients treated for epilepsy at the University of Washington Medical Center. A week before surgical resection of cortical tissue, subdural grid electrodes were implanted over the central and temporal cortex to provide estimates of the location of epileptic foci and to map the sensory and motor sites. The location of the central sulcus was estimated from motor responses evoked by stimulation and from somatosensory evoked potentials recorded at various sites (Ojemann and Engel, 1987). After the subject recovered from implantation surgery, recordings were made from electrodes overlying the sensorimotor cortex while the subject performed a 2-dimensional tracking task. This consisted of following a moving target on a video screen with a cursor controlled by a hand-held joystick. Surface EMGs were monitored over the forearm and digit muscles. ECoG, EMG and cursor movements were recorded on magnetic tape for subsequent analysis.

Data Analysis

To monitor changes in oscillatory activity, power spectra of LFPs were calculated for 256-msec windows which were shifted successively by 100 msec. Average power in different bands was plotted as a time series along with LFPs (and EMGs if available), allowing changes in power to be correlated with behavior. To document the activity associated with oscillatory cycles, we calculated cycle-triggered averages (CTA) of LFPs and EMG activity, and histograms of unit activity aligned on the cycles of LFP oscillations (Murthy and Fetz, 1992). Since oscillatory episodes in the LFP occurred during a small proportion of total recording time, the CTAs captured the patterns of unit firing and associated LFPs specifically during LFP oscillations.

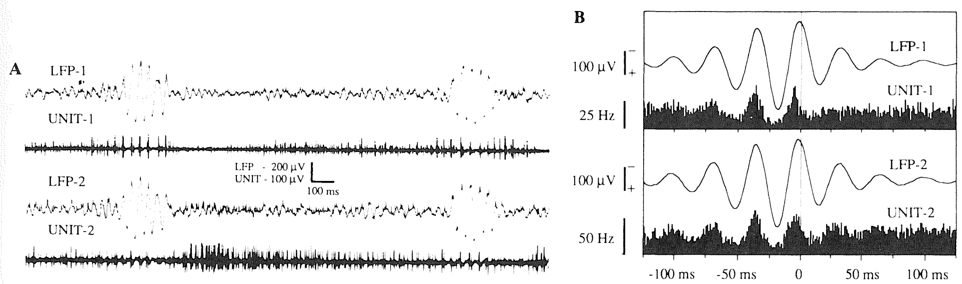

Figure 1. (A) LFPs and unit activity recorded in the motor cortex with two electrodes separated by ~800 mm. The monkey was retrieving a raisin from a Klüver board. (B) Cycle-triggered averages of LFPs and unit activity aligned on the cycles of LFP-2. (From Murthy and Fetz, 1992.)

Pairwise cross-correlations of LFPs (digitized at 1 kHz) from different sites were also performed to quantify the extent of synchronization. Correlations were calculated for time windows of 200 msec, successively shifted by 100 msec. For each window, the peak correlation closest to 0 delay and the corresponding time shift were obtained. A probability distribution of the correlation peak amplitudes (one point from each 200-msec segment) was made for recording epochs of up to 50 sec. This distribution was integrated to yield a cumulative probability distribution. Since high correlations could occur purely by chance, especially if the two correlated signals had similar frequencies, we determined a significance level by the following procedure. For the same recording epochs, cross-correlations were recalculated with one of the channels shifted by a time interval much larger than the oscillatory episodes, usually 1 sec. From the cumulative distribution of the "shifted" correlations, the significance level for the regular correlations was taken as the level below which 95% of the "shifted" correlations lay.

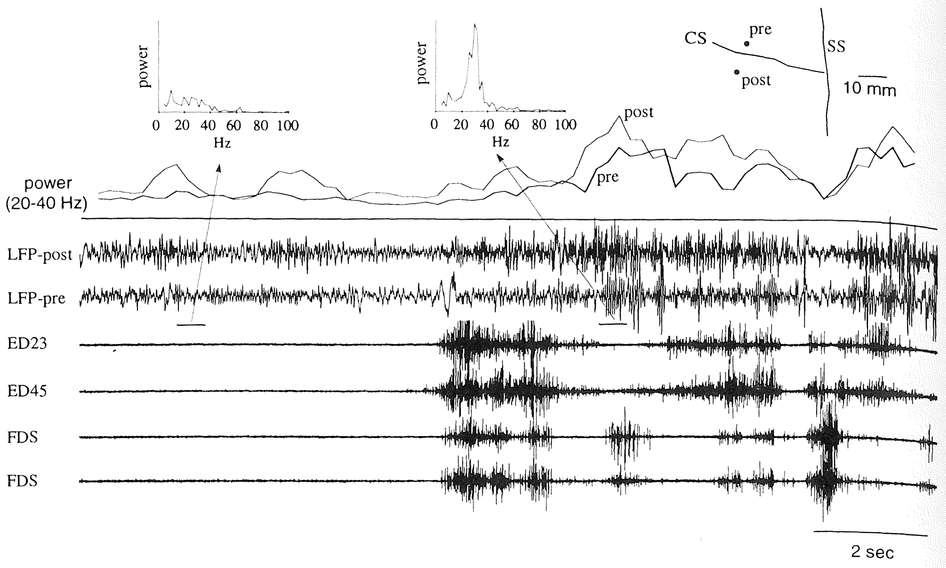

Figure 2. Pre- and post-central LFPs and EMGs of contralateral muscles recorded while the monkey was reaching to the side of its head to wrest a raisin from the experimenter's hand. For both LFPs the power in the 20-40 Hz band (calculated for 256-msec windows that were shifted successively by 100 msec) is plotted above the LFPs. After an initial period when the monkey was sitting quietly without any overt movement, a raisin was offered to the side. When the monkey reached for the raisin, oscillations increased at both cortical sites. Insets show the power spectra for precentral LFP at times indicated by the horizontal bars. Right top indicates the approximate location of the recorded sites.

RESULTS

Properties of Oscillations

Figure 1 shows examples of LFP and unit oscillations in the hand area of the motor cortex of a monkey retrieving a raisin from a Klüver board. During oscillatory episodes, the power in the 20-40 Hz band increased by more than 10 times above the baseline. When clear oscillations appeared in the LFP traces, the units fired in bursts during the negative deflections in LFP; these units were also active in the absence of LFP oscillations. CTAs of LFPs and units shown in Fig. 1b confirm the synchrony between the LFP oscillations and the firing of units. In order to correlate the occurrence of oscillations with movement, we recorded EMGs from forearm muscles simultaneously with LFPs from pre- and post-central sites. During the premovement period, when the monkey was waiting with its arm unrestrained (and the EMGs were silent), there was little oscillatory activity (Fig. 2). When the monkey was presented with a raisin to the side of its head, it attempted to wrest it from the experimenter's hand. Oscillations appeared at both pre- and post-central recording sites, although these episodes were not time-locked to the onset of EMG. During this period of exploratory movements, oscillations occurred much more frequently than in the quiet period. The following parameters of the oscillations were compared under different behavioral conditions: the average number of cycles per oscillatory episode, the mean frequency of oscillations within episodes, and the number of oscillatory episodes per second. The mean number of cycles per episode (4.5) and the mean frequency of oscillations (27 Hz) remained similar across behaviors, but the number of oscillatory episodes per second was different (Murthy and Fetz, 1992). When the monkey was quiet or performing the overtrained flexion-extension task, oscillations occurred at a rate of 0.2 per second; during unconstrained exploratory movements their occurrence increased to almost 1 per second (Fig. 3). There was no consistent relation between the bursts of EMG and LFP oscillations, but CTAs of rectified EMGs often revealed an oscillatory modulation synchronized with the LFP oscillations (Murthy and Fetz, 1992).

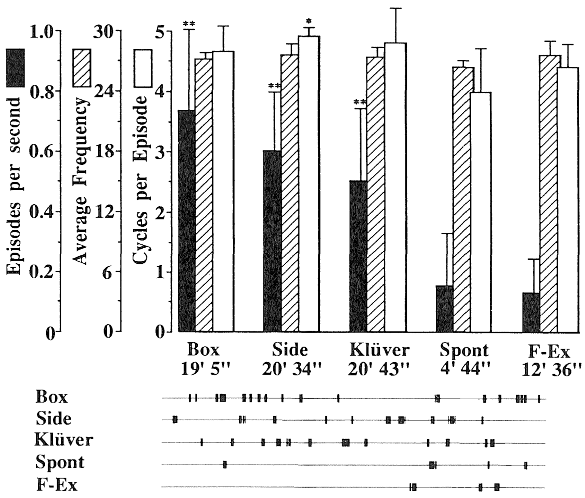

Figure 3. Parameters of LFP oscillations for different behaviors. The number of cycles per episode, episodes per second, and average cycle frequency were calculated as described (Murthy and Fetz, 1992). The amount of recording time for each behavior is indicated below each set of bars. Shown below are triggers from cycles of oscillations for a typical 20-sec period for each behavior. Behaviors were: Box, retrieving food pieces from a box at the level of the hip outside the range of vision; Side, retrieving pieces of food from the experimenter's hand at the side of the monkey's head; Klüver, retrieving pieces of food from the slots of a Klüver board; F-Ex, alternating flexion and extension of wrist; Spont, quiet sitting, no overt movement. (From Murthy and Fetz, 1992.)

Synchronization Between Sensory and Motor Cortical Sites

The LFP oscillations could occur synchronously over a wide area of the sensorimotor cortex. Ipsilaterally, the oscillations could become synchronized between pre- and post-central sites (Fig. 4). There was no detectable change in the phase of oscillations from anterior to posterior sites. However, traveling waves of oscillations similar to those suggested to occur in humans (Ribary et al., 1991) would have a velocity too large to generate significant phase shifts for spatial separations of our electrodes (time shifts would have been less than 1 msec). Synchronization of LFP and multiunit activity in the postcentral and precentral sites suggests that coherent oscillations affect large populations of neurons and may play a role in associating their activity.

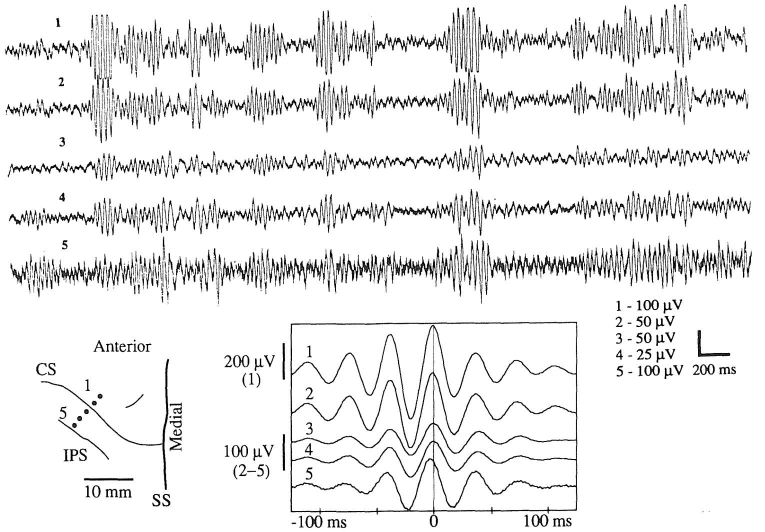

Figure 4. LFPs recorded simultaneously at five sites in pre- and post-central cortex (indicated on the sketch of cortex at bottom left) when the monkey was reaching for a raisin offered to the side of its head. Oscillations occurred synchronously at all sites, with negligible phase shift, as confirmed by cycle-triggered averages aligned on the cycles of LFP-1 (lower right). (From Murthy and Fetz, 1992.)

Synchrony and Behavior

If the oscillations play a role in associating activity at specific sensory and motor areas, the synchronization of oscillations at different sites could depend on behavioral context. This associational hypothesis would predict that different cortical sites may exhibit independent oscillations, which become synchronized preferentially during those particular behaviors that require coordination of neural responses at these sites. To test this hypothesis we recorded LFPs at two independent sites simultaneously, in pre- and post-central sites in the distal arm representation area, while the monkey (1) rested quietly without any overt movement, (2) performed the overtrained wrist flexion and extension task, and (3) performed reaching movements to retrieve raisins from unseen locations. As previously described, the oscillations occurred more often during unconstrained reaching movements than during repetitive trained movements. For the same recordings, cross-correlations between pairs of LFPs and the autocorrelations for each LFP were calculated for each behavior. If either site or both sites exhibited LFP oscillations, as judged by the magnitude of the secondary peak in the autocorrelations, the corresponding cross-correlation peak was measured; the average values are plotted in Fig. 5. More correlation peaks were included in the average for periods of reaching movements than for the other two periods because oscillations were much more likely during periods of reaching.

However, the mean amplitudes of the correlation peaks and the proportion of oscillatory episodes that were synchronized were similar for the different behaviors (Fig. 5).

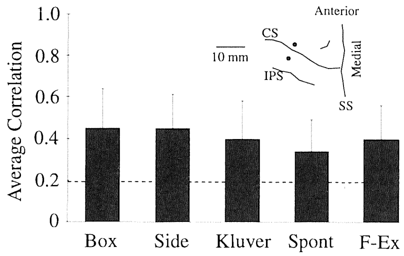

Figure 5. Amplitudes of peaks of cross-correlations between LFP oscillations recorded at a pre- and post-central site in the hand representation, during different behaviors. For each 200-msec window cross-correlations and autocorrelations of both signals were calculated. If either or both autocorrelation had a secondary peak above 95% significance level (usually 0.5), the magnitude of the cross-correlation peak for that window was included in the average. The significance level calculated from shifted correlations was 0.19 and is indicated by the dashed line. Behaviors indicated are the same as in Fig. 3.

Bilateral Synchrony

Recent experiments in the visual cortex of cats have indicated that activity of neurons in the two hemispheres could become synchronized, and that the synchronization was mediated at least in part by callosal connections (Engel et al., 1991; Munk et al., 1992). Primates commonly perform synergistic bimanual movements, which probably involve interhemispheric cortical interactions. To test whether oscillations in the sensorimotor cortex are involved in mediating this interaction, we recorded bilaterally in a monkey while it made manipulatory movements with either hand alone and with both hands together. LFPs and multiunit activity were recorded simultaneously at two homologous sites bilaterally in the hand representation of the motor cortex. The monkey manipulated unshelled peanuts with either the right hand alone (left hand restrained), or vice versa, and with both hands. EMGs were also recorded from a flexor and extensor muscle in each forearm. The occurrences and parameters of the LFP oscillations at both sites were documented, as was the synchrony between them.

As shown in Fig. 6, oscillations occurred in both hemispheres when the monkey made bimanual movements. However, oscillations occurred in both hemispheres even when the monkey made movements with one hand alone. The frequency of occurrence of oscillatory episodes in either hemisphere when the monkey used both hands was the same as during unimanual activity. Synchronization of LFPs was determined by calculating cross-correlations for 200-msec windows shifted by 100 msec. The cumulative distributions of correlation peaks over a period of 40 sec each when the monkey was actively making manipulatory movements with the left hand, the right hand, and both hands were very similar (Fig. 6b).

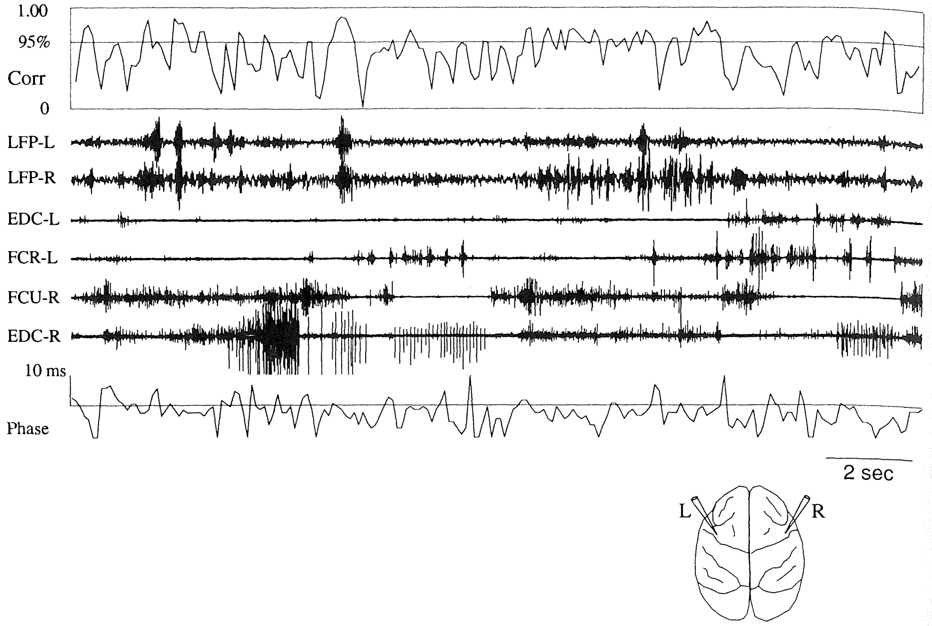

Figure 6 A. LFPs recorded at homologous sites in the left and right motor cortex (indicated in the sketch of the cortex) and EMGs from left and right hand muscles while the monkey manipulated an unshelled peanut with both hands. Cross-correlation peaks (Corr, top) and the corresponding time delays from zero (Phase, bottom) were calculated for 200-msec windows (100-msec shift between successive windows). Oscillations occurred at both sites and could become synchronized with negligible phase-shift. The 95% significance level determined from "shifted" correlations was 0.65 and is indicated by the horizontal line labeled 95% level.

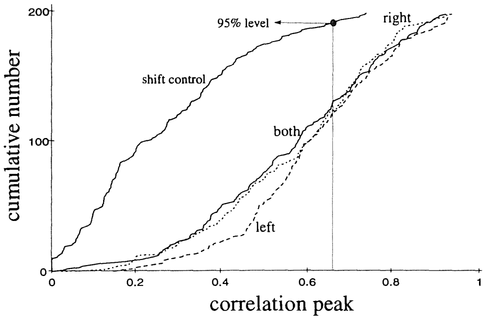

Figure 6 B. Cumulative distributions of the amplitudes of correlation peaks for 40-sec recordings under each condition of uni- or bimanual manipulations. The shift control distribution was obtained by shifting the left LFP forward by 1 sec, recalculating the correlations for all three conditions, and taking the average.

If synchronization of LFPs had increased preferentially during the bimanual task, the distribution of correlations during this task would have shifted to the right in comparison with those for either hand alone. The lack of such a shift suggests that bilateral synchronization of LFP oscillations may not be preferentially correlated with overt bimanual movements. This does not rule out the possiblity of more specific synchronization of smaller groups of neurons at a finer temporal resolution, which may not be reflected in LFPs. Cross-correlating simultaneously recorded single- and multi-unit activity at different sites would be required to resolve this.

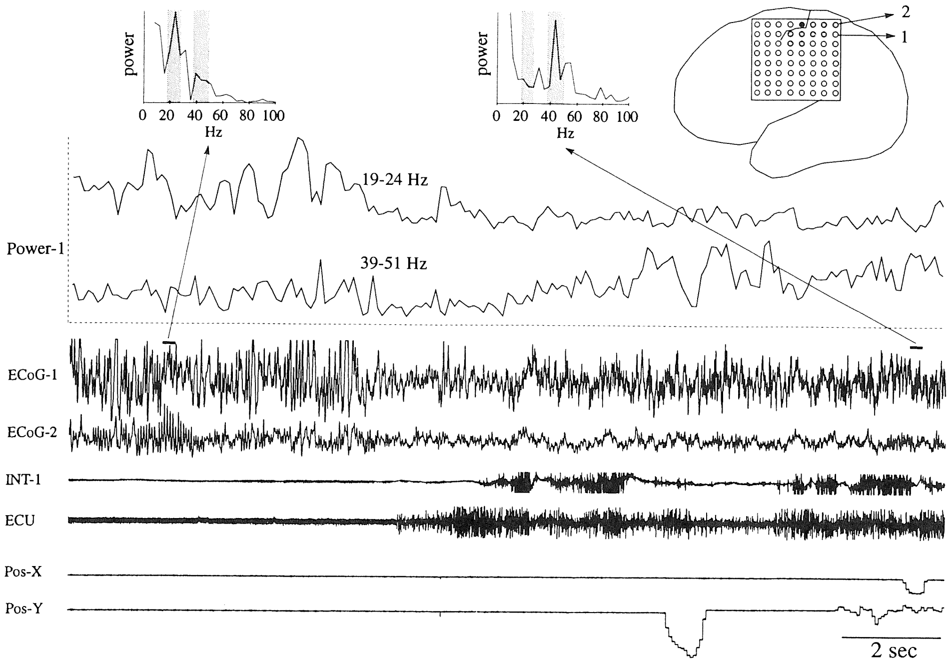

Figure 7. Subdural recordings from a patient while he was tracking a visual target on a video screen with a hand-held joystick. Right top shows the approximate location of the electrode grid. The black dot indicates a site whose stimulation evoked movement of the contralateral hand and the grey shaded dots indicate sites that showed somatosensory evoked potentials from the contralateral hand and arm. Recordings include: ECoGs from sites 1 and 2 (ECoG-1 and -2); surface recordings of EMGs from thumb (INT-1) and wrist extensor (ECU); and the 2-dimensional position of the joystick. For ECoG-1 the power in the two bands indicated was calculated for 256-msec windows (shifted successively by 100 msec), and is plotted above the ECoGs. Power spectra are illustrated for two windows taken during the waiting and tracking periods with the same relative scale. Shaded areas indicate the frequency bands for which power is plotted. After the onset of tracking, power diminished in the 20-Hz range and increased in the 39-51 Hz band.

In order to confirm that the recordings at bilateral sites were independent and not merely volume-conducted signals from distant sources, we calculated CTAs of neurons recorded at both sites aligned on the cycles of LFP oscillations at one site. In 34 of 43 pairs of recordings, averages indicated oscillatory modulation of units at both sites, confirming the presence of local generators of synchronized rhythmic activity in each hemisphere.

Oscillatory Activity in Human Electrocorticograms

Techniques for recording ECoG directly from surface of sensorimotor cortex (Ojemann and Engel, 1987) provide an opportunity to determine whether high-frequency oscillations similar to those described above occur in humans during movements requiring fine sensorimotor control. The existence of 20-30 Hz rhythms in scalp EEG over sensorimotor areas has been documented (Jasper and Penfield, 1949; Pfurtscheller, 1981), but their correlation with motor behavior has not been studied extensively. In collaboration with Dr. George Ojemann, we were able to monitor subdural ECoG at multiple sites, with better spatial resolution of signals than obtained with EEG. Multichannel ECoG recordings from the sensorimotor cortex were obtained from two patients when they performed a visuomotor tracking task using the hand contralateral to the recorded cortical hemisphere. The results from the two subjects were quite similar and detailed analysis is presented for one subject (Fig. 7). When the subject was prepared to begin the task, but made no overt movement of the hand, high-amplitude rhythmic activity around 20 Hz was observed in the channels overlying the sensory cortex. When he began the tracking task, the 20-Hz activity was suppressed over the sensorimotor areas. Simultaneously, higher frequency oscillations around 40 Hz appeared in one channel posterior to the estimated location of the central sulcus. The 20-Hz reduction was also observed when the subject made a forceful pinching movement with his thumb and forefinger after a period of waiting. However, the pinching task produced no significant increase in the 40-Hz oscillations. This suggests that the reduction in the 20-Hz rhythm may be a general effect spread over the entire sensorimotor area, but the increase in the 40-Hz rhythm may be more specific to the motor task performed.

DISCUSSION

Although there is now ample evidence of widespread oscillatory activity in the cortex, there is little agreement about its possible function. High-frequency cortical oscillations in the range of 20-70 Hz occurring in sensory areas are thought to play a role in perception. Synchronous rhythmic activity in the visual cortex was postulated to bind different stimulus features of a single object and to represent it as distinct from other objects in the visual field (Eckhorn et al., 1988; Engel et al., 1992; Singer, 1993). In support of this hypothesis, oscillations have been shown to be synchronized between different visual cortical areas and between two hemispheres of the cat in a stimulus-specific manner (Engel et al., 1991). In the sensorimotor cortex, 20-40 Hz oscillations occur across a wide area and have been correlated with certain behaviors (Murthy and Fetz, 1992). In overtrained tasks, LFP oscillations were relatively rare during the actual movements (Murthy and Fetz, 1992; Sanes and Donoghue, 1993). However, in a delayed response task oscillations were evident during the waiting period before movement began (Sanes and Donoghue, 1993). When the monkeys made less constrained exploratory movements to retrieve food, oscillations occurred more frequently (Murthy and Fetz, 1992). Oscillations were not reliably associated with every movement, indicating that they are not essential for execution of movements. Rather, their general increased rate of occurrence during interactive movements suggests a higher-order role in sensorimotor integration.

Oscillations could become synchronized over wide areas in the primary motor cortex, between motor and sensory cortex, and between the motor cortices of the two hemispheres. Synchronization of LFP and multiunit oscillations in pre- and postcentral sites could be a possible substrate for sensorimotor integration. During exploratory tasks, sensory feedback would be essential to make precise movements (Asanuma and Arissian, 1984). Under these conditions, rhythmic synchronous activity could lead to efficient excitation of neurons that are part of the same functional network. There are abundant anatomical connections between pre- and post-central cortex (DeFelipe et al., 1986). A close functional link between the two areas is also supported by close similarities in response properties of precentral and postcentral neurons, with regard to sensory input and motor-related activity (Fetz, 1984). Our findings suggest that synchronization of spike discharges of neurons in the two areas could be a further substrate for functional interaction.

Synergistic bimanual movements most likely involve neural interactions between the two hemispheres through callosal or commisural connections. While the supplementary motor area has been suggested to be important for mediating bimanual synergies (Brinkman, 1984; Wiesendanger et al., 1992), there is clear evidence that the primary motor cortex also plays an active role (Tanji et al., 1988; Aizawa et al., 1990). Some motor cortex neurons respond with ipsilateral movements (Tanji et al., 1988), and stimulating certain sites in the motor cortex elicits bilateral hand movements (Aizawa et al., 1990). We found that LFP oscillations occurred at bilateral sites for unimanual as well as bimanual movements. LFP oscillations at bilateral sites could become synchronized with negligible phase shifts during bimanual manipulations. Further, single- or multi-unit activity could become synchronized with the LFP oscillations. Interestingly, synchronization of LFP oscillations was just as likely and just as strong for unimanual manipulations as for bimanual ones, suggesting that synchronization was not specific for bimanual coordination. However, since LFPs are complex averages of underlying neural activity, they may not be appropriate indicators of synchronization of small groups of neurons. Smaller groups of neurons may exhibit transient and specific synchronization for bimanual tasks which may not be detected by average measures such as LFPs.

Widespread synchronization of LFP oscillations in the sensorimotor cortex appears to be too nonspecific and episodic to be involved directly in motor control, particularly when compared with the specificity of synchronization in the visual cortex (Engel et al., 1992). However, the complexity of motor cortical organization with its convergent and divergent cortico-cortical and corticofugal projections could account for the extent of synchronization. Low-threshold intracortical microstimulation of multiple disjoint sites in the primary motor cortex can evoke similar digit-muscle responses (Sato and Tanji, 1989). Correlational evidence indicates that single corticomotoneuronal cells can have postspike effects on multiple muscles, both agonists and antagonists (Fetz and Cheney 1980). More directly, single axons of pyramidal tract cells have been shown to arborize among different motoneuron pools in the spinal cord (Shinoda et al., 1981). Sites that evoke movement across different joints are connected by intrinsic axon collaterals in a complex manner (Huntley and Jones, 1991). These connections could provide an anatomical basis for the synchronization of LFP oscillations over the entire arm representation. Since most natural movements of the hand and the arm involve coordination of many muscles, widespread synchronization of LFP oscillations may provide a general increase in excitability to allow recruitment of more specific neurons for an upcoming movement. Other observations further support the idea that oscillations may play a general role in attention, rather than a specific role in movement control.

Single units in the motor cortex discharge reliably at the onset of and during particular movements. In contrast, LFP oscillations were not consistently correlated with occurrence of EMG bursts. However, CTAs of EMGs revealed oscillatory modulation of EMGs synchronized with LFPs (Murthy and Fetz, 1992). This suggests that even if the oscillatory episodes are not reliably timed to the execution of movements, they nevertheless involve output cells that can influence muscle activity. Precisely timed synchronous inputs to spinal circuits might allow subtle yet fast modification of ongoing muscle activity, especially during fine finger movements. Further, during attentive periods before movement begins synchronous oscillations could help bring functionally related neurons close to firing threshold and facilitate their response to subsequent inputs.

Oscillations could also play a role in modulating synaptic efficacy among neurons that are active simultaneously. The synaptic inputs that arrive during the depolarizing phase of the oscillations could be potentiated selectively. In the hippocampus, in-phase stimulation of afferents to CA1 during carbachol-induced theta rhythm can lead to long-term potentiation (Huerta and Lisman, 1993). Preliminary data from our lab indicate that evoking excitatory postsynaptic potentials (EPSPs) in cortical neurons in phase with the negative deflections of naturally occurring LFP oscillations can transiently potentiate the EPSP (Chen and Fetz, 1993).

We found that oscillations similar to those described in monkeys occurred in the sensorimotor cortex of humans during performance of sensorimotor tasks. In light of the results from the monkey experiments, we asked the human patients to perform a task that involved ongoing sensorimotor integration instead of repetitive movements. We found that the power in the 20-Hz band decreased at the onset of both finely controlled movement and simple forceful pinching of the digits; however, 40-Hz power increased robustly only during the tracking task. This is consistent with a recent report that in addition to a decrease in the 20-Hz rhythm, there was an increase in power near 40 Hz in the EEG at the onset of movement (Pfurtscheller and Neuper, 1992). Although the occurrence of these oscillations during sensorimotor tasks suggests some similarities with oscillations in monkey cortex, there were clear differences. In humans, high-frequency oscillations were most prominent over the postcentral cortex, whereas in monkeys oscillations were usually more robust in the precentral cortex. Second, ECoG in human sensorimotor cortex exhibited a clear shift in frequency from around 20 Hz during the preparatory phase to around 40 Hz during actual movement, but such shifts were not obvious in monkeys (Sanes and Donoghue, 1993). Further, the 40-Hz oscillations in humans were spatially restricted to one or a few electrode sites; oscillations in monkeys were more widespread. In this respect, the 20-Hz oscillations in humans were similar to the 20-40 Hz oscillations in monkeys because: (1) they both occurred over a wide area of cortex, and (2) they both occurred during preparatory phases of movements and were suppressed at the onset of movement in a delay task (Sanes and Donoghue, 1993). Further experiments are required to determine the differences and parallels between oscillatory activity in monkeys and humans.

In summary, we have considered three possible roles for the synchronous 20-40 Hz oscillations in sensorimotor cortex. First, they could play a role in associating neurons that are coactivated during a task and facilitate interactions in functional networks of neurons. Second, they could simply reflect an increased excitability of neurons caused by a general increase in the attentional or arousal state of the animal. Third, they could play a role in altering synaptic transmission. Our evidence from multiple site recordings in monkeys does not appear to support the first hypothesis since we have been unable to find preferential synchronization of oscillations during behavior involving neurons at the relevant sites. The second possibility is more compatible with our data since oscillations occur more frequently over a wide area of the cortex during exploratory movements requiring attention. The third hypothesis is supported by preliminary data (Chen and Fetz, 1993), but remains to be further explored.

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