

Oscillations in local field potentials of the primate motor cortex during voluntary movement

(neural oscillations/local neural circuits/instructed voluntary movements/forearm/monkeys)

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ABSTRACT We investigated the occurrence and distribution of oscillatory activity in local field potentials (LFPs) recorded from the frontal motor cortex of behaving monkeys performing skilled voluntary movements. LFPs were recorded simultaneously from up to 12 sites distributed throughout motor cortex while monkeys performed a visually guided, instructed delay task using the wrist or digits. Oscillatory activity between 15 and 50 Hz was evident in the LFP recorded from both primary motor cortex and premotor areas. Oscillations occurred preferentially before the visual cue to initiate movement but were infrequent during movement. Oscillations typically stopped before movement initiation during the wrist task, although they often continued into the initial phases of movement during the digit task. The relationship of oscillations to task performance was consistent across trials over periods of many months, although the amplitude and duration of oscillations varied across trials and days. Interactions between pairs of LFP recordings, evaluated with cross-correlation analysis, revealed synchronous oscillations over long distances (>7 mm) and across primary motor cortex and premotor recording sites. These studies demonstrate that oscillations recorded in the LFP in motor cortex during trained motor tasks are not related to the details of movement execution but may be related to aspects of movement preparation.

Oscillatory activity of single neurons, of multiunit activity, and of local field potentials (LFPs) in the 20- to 50-Hz range occurs in a variety of cerebral cortical structures including mammalian olfactory (1), visual (2–6), somatic sensory (7), and motor (8–10) cortex. Oscillations in LFPs or multiunit activity obtained from visual cortex (3) may reflect synchronized activity of local neuron assemblies related to information processing in these areas. Further investigations have revealed synchronization of multiunit oscillations in homologous regions of visual cortex in the two hemispheres (11) and in separate areas of visual cortex within one hemisphere (12). Correlation of neural activity in widely separated visual cortical areas may be a neural implementation of feature binding that could produce unified perception of a complex sensory stimulus (13, 14).

A number of cerebral cortical areas are closely related to planning and performing voluntary movement (15). The primary motor cortex (MI) is most closely tied to aspects of execution, whereas premotor areas appear to have a greater role in motor planning. Neural oscillations in cortical motor areas could reflect specific aspects of activity related to motor planning and performance or to sensory input. Oscillatory rhythms in field potentials have long been known to exist in motor cortical areas (16). They have been associated with aspects of attention and with movement. In cats and monkeys, “fast rhythms” reportedly occur during attentive

states and terminate with movement (16), but more recently, Murthy and Fetz (9) reported the occurrence of LFPs and unit oscillations in the 25- to 35-Hz range in MI while monkeys performed arm movements. These workers noted that oscillations occurred more frequently during free reaching, especially when the animals reached for objects outside the visual field. Oscillations occurred less frequently during repetitive movements or during immobility. However, none of the previous studies used motor tasks that permitted an assessment of how neural oscillations in motor cortex relate to features of attentiveness, preparation, and performance occurring in a learned motor task. Furthermore, previous studies concerning neural oscillations in motor cortex typically recorded activity from single sites; the synchronization of activity across motor cortical areas during preparation and execution of movement was not assessed. In the current experiments, we examined LFPs recorded simultaneously from up to 12 sites across MI and premotor area (PMA) while monkeys performed wrist or digit movements in a visually guided, step-tracking task with an instructed delay. We found that 15- to 50-Hz oscillations in the LFPs were most prominent before movement onset, but their onset time was not correlated with occurrence of instructional cues. By contrast, the cessation of LFP oscillations was correlated over wide areas with movement onset. Oscillations were correlated between sites related to different joints of the arm and in different subdivisions of the frontal motor cortex. The strength of correlation had no relationship to the distance between recording sites.

MATERIALS AND METHODS

Two male monkeys (*Macaca fascicularis*) weighing 4–5 kg used visual cues in an instructed delay task either to perform wrist flexion movements or downward-directed finger flexor force. The animals sat in a primate chair positioned in front of a computer-controlled video screen with the right forearm gently restrained. For wrist movements, the hand was placed between two padded plates with the wrist coaxial with the axis of a torque motor. Wrist movements were performed against a mild spring load, and a video screen displayed targets for the monkey to acquire by positioning a cursor representing wrist angle. For each trial, the monkeys positioned the hand at $\approx 15^\circ$ of wrist flexion for 3–4 sec. After 1–2 sec of holding without instructions (the hold period), a pre-cue target appeared for 2–3 sec on the video screen to instruct the location of the upcoming 25° or 45° flexion movement (the pre-cue period). The monkey was instructed to move when the go-cue target changed appearance. For the digit task, the monkey held the right hand on a plate mounted to a strain gauge using the same visual cues as for the wrist task. The initial force was minimal or zero, and the new force target was signaled by a pre-cue. The monkey was required

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Abbreviations: LFPs, local field potentials; MI, primary motor cortex; PMA, premotor area.

to attain a new wrist position or digit force within 1 sec of the go cue and to hold the new position or force for 500 msec to receive a liquid reinforcement.

After the monkeys consistently received liquid on 85% of the trials, recording wires were surgically implanted in the motor cortex using sterile procedures and inhalant anesthesia (Isoflurane). Monkeys were mounted in a stereotaxic instrument, and a craniotomy was made over the motor cortex. The dura mater was resected, and up to 25 wires (50- μ m diameter PtIr wire, coated with 10- μ m Teflon) were inserted into the cortex between the central and arcuate sulci and to depths consistent with layer V. After insertion of all wires, the set of electrodes and the cortical surface were covered first with Fibrin glue (Immuno US, New York), and then the entire assembly, including anchor screws and a connector, was covered with dental acrylic.

Neural Activity Recording and Analysis. A 25-channel headstage preamplifier (Microprobe, Clarksburg, MD) was mounted directly on the monkey's head. The headstage output was led to Grass Instruments AC-coupled amplifiers and then to a 16-channel Vetter videotape signal conditioner. For further categorization of recording sites, the cortex was stimulated with trains of stimuli (333-Hz trains, 30-msec duration, 200- μ sec pulses) using currents up to 60 μ A.

For analysis of the LFPs relationship to behavior, hand position or digit force and up to 12 channels of neural data were digitized from videotape at 2.5 kHz (LFP-filtered at 10–100 Hz, 3 decibel points) and in epochs of 6.6 sec, beginning at the onset of each movement cycle. The LFPs were low-pass filtered digitally (flat region = 0–52 Hz; 3 decibel point = 62 Hz; 20 decibels down at 70 Hz). The frequency spectrum for each waveform was derived with standard fast Fourier transforms, and a sliding spectrogram (256-msec epochs, 25-msec steps) between 15–45 Hz in 5-Hz bands was computed. Auto- and cross-correlograms and sliding (256-msec epochs, 50-msec steps) auto- and cross-correlograms were computed.

RESULTS

Monkey FC was studied over an 18-mo period. Of 17 wires implanted in motor cortex, electrical stimulation evoked contralateral arm movements at 11 sites; the remainder showed head or leg movements or no effect. Recordings were obtained from 14 sites. Monkey FD, studied for 6 mo, had 25 implanted wires. Movements were evoked by stimulating 23 wires; arm movements were evoked at 17 sites, whereas recordings were obtained from 18 wires.

Microwire Location. Histological evaluation of wire placement is currently unavailable because the two monkeys from which neural activity reported upon in this paper was obtained are still participating in experiments. From surface reconstruction of wire placement obtained during implantation and the electrical stimulation results, it would appear that most wires are located in the MI arm area or in area 6 immediately posterior and medial to the genu of the arcuate sulcus, commonly termed PMA.

General LFP Characteristics. LFPs recorded at most motor cortex sites exhibited oscillatory activity (Fig. 1). In monkey FC, oscillations did not occur at a MI leg site, and they were weak at one MI wrist site and at two PMA sites related to neck and head movement. Oscillations in monkey FD occurred at leg sites but were weak at three MI wrist and digit sites. There was no obvious difference in the presumed location or depth of nonoscillating and oscillating sites. Oscillations were similar for FC and FD at topographically different locations within MI and PMA. LFP oscillations could be episodic or sustained, and durations of several seconds were evident. The longest sustained period of oscillation endured throughout the 6- to 8-sec period of the

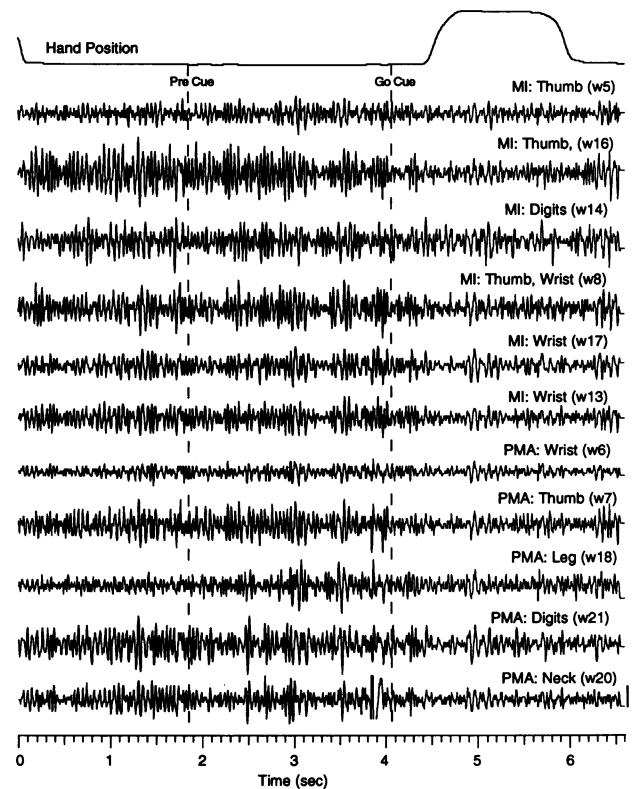


FIG. 1. LFPs during instructed delay task. LFP recordings from 11 wires implanted in motor cortex of monkey FD during a wrist movement. The top record displays hand position and the LFP recorded from each MI and PMA site. Each recording is identified with the low threshold movement evoked by intracortical electrical stimulation and an identification code. Note the diversity of LFP oscillations in the various records, from relatively brief bursts of LFP synchrony (wire 18, from 3 to 4 sec) to sustained synchrony in several recordings (e.g., wires 7, 8, and 16). Note that oscillations and high amplitude diminish after the go cue and remain suppressed throughout the hand movement. (LFP calibration = 100 μ V.)

instructed delay task, although waxing and waning of amplitude were observed during such episodes.

Fig. 2 illustrates multiple examples of LFPs obtained from one site examined across nearly 15 mo when monkey FC performed either the wrist (A_1 – A_5 and B_1 – B_2) or digit (C_1 – C_3) task. As shown here, the duration, magnitude, and precise time of occurrence of the oscillations varied somewhat from trial to trial and day to day. Threshold electrical stimulation at this MI site evoked thumb extension and wrist extension.

Occurrence of LFP During Tasks. Oscillations showed certain consistent relationships to behavior across the two monkeys and two tasks (Figs. 1–3A, 4B). At most recording sites, oscillations were most pronounced during the hold and pre-cue periods. The oscillations declined markedly around movement onset and remained suppressed during the movement. There was a noteworthy difference in the timing of cessation of LFP oscillatory activity for the two tasks. Although obvious oscillations generally ceased before wrist-movement onset, they often continued for a short time after onset of digit force (compare traces in Fig. 2 A and B with those in C). Oscillations rarely occurred during the dynamic phase of wrist movement, although they sometimes reappeared during the subsequent static hold; at this time the oscillations were usually of lower amplitude and shorter duration than observed before movement onset (right sections of Fig. 1). For both tasks, oscillations were again prominent when the monkey returned to the holding position to begin the next trial. The pre-cue, which signaled the extent

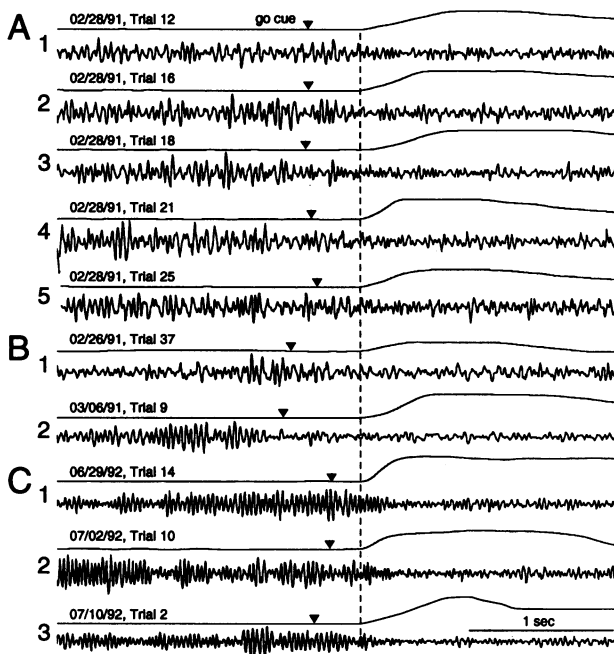


FIG. 2. Reproducibility of LFP oscillations. Recordings from one wire implanted in MI of monkey FC and kinematic records (upper of pair) obtained during seven wrist movements (A and B) and three digit motor actions (C). All records are aligned on movement onset with the go-cue onset indicated by the downward pointing triangle. (A) Records from a set of 100 trials when the monkey performed single-amplitude wrist-flexion movements. (B) Records from a recording session 2 days earlier (B₁) and one session 6 days later (B₂) than those in A but while the monkey performed either shorter or longer wrist movements. (C) A record from each of 3 days >1 yr later than those from A and B but while the monkey worked in the digit task. For all records, the LFP oscillations were most evident before the go cue and declined either before movement onset (wrist) or in the early stages of movement (digit). (LFP calibration = 100 μ V.)

of the upcoming movement, appeared \approx 2 sec later. In the vast majority of cases there was no striking change in the appearance of oscillations before or after the pre-cue appeared. Thus, there was no strict temporal correlation between visual cues and oscillatory episodes. It is also noteworthy that, although task conditions varied in the hold and preparatory periods (i.e., regarding visual cueing), there was no obvious or consistent manifestation in the monkey's behavior that indicated a change in set or attention between these two premovement periods. Despite the visual cueing, the monkey sometimes failed to perform, and oscillations during these trials typically continued until the next movement sequence.

Similar to observations by others in visual cortex (3) and MI (9), the frequency of LFP oscillations was in the 15- to 50-Hz range. The dominant frequencies differed for the two monkeys. In initial recordings from monkey FC, the dominant frequency clustered around 28 Hz, whereas that for monkey FD clustered around 20–25 Hz. When monkey FC switched from the wrist to the digit task, the dominant frequency clustered around 35 Hz, but no similar frequency shift occurred in monkey FD. Presently, we do not know why oscillation frequency during the digit task was higher only in monkey FC.

During a single trial, the dominant frequency of oscillations was similar across wires. However, peak frequency variations of a few Hz occurred between different trials, although this variation had no evident relationship to active motor behavior. By contrast, frequency spectrograms in 5-Hz bands between 15 and 45 Hz revealed subtle differences in the waxing and waning of frequency across recording sites during

a trial (Fig. 3). At some sites, LFP frequency modulation was most evident within a relatively narrow bandwidth, suggesting that different forms of information could be carried over restricted frequency ranges in the LFP.

Cortical Interactions. We used cross-correlation methods to examine relationships of oscillatory activity occurring simultaneously at various recording sites. Fig. 4 illustrates "correlograms" calculated for LFP recorded at five motor cortex sites during one wrist movement. Each of these sites was classified either as a digit or a wrist site, according to the electrical stimulation effects. Two types of interactions are depicted. First, the insets above the right side of each histogram show the cross- or auto-correlograms computed while the monkey performed one wrist movement. The correlograms indicated a range of interactions from absence of interaction (data not shown) to a high degree of synchrony. We found that the strength of correlation did not depend upon propinquity of recording sites. Oscillations occurring in two sites distant from each other, even in different cortical motor areas, could be highly correlated. For example, activity at site 7 in PMA, a "thumb" site, and site 8 in MI, a "thumb and wrist" site, was highly correlated, even though the sites were separated by more than 3 mm (measured along the cortical surface) and had different evoked movement effects. By contrast, wires 7 and 13 were separated by 1.6 mm, but their oscillations were less strongly correlated.

A second analysis correlated activity between pairs of LFP recordings in successive 256-msec epochs stepped at 50 msec across the entire behavioral period (histograms in Fig. 4A). LFPs recorded at several pairs of motor cortical sites showed

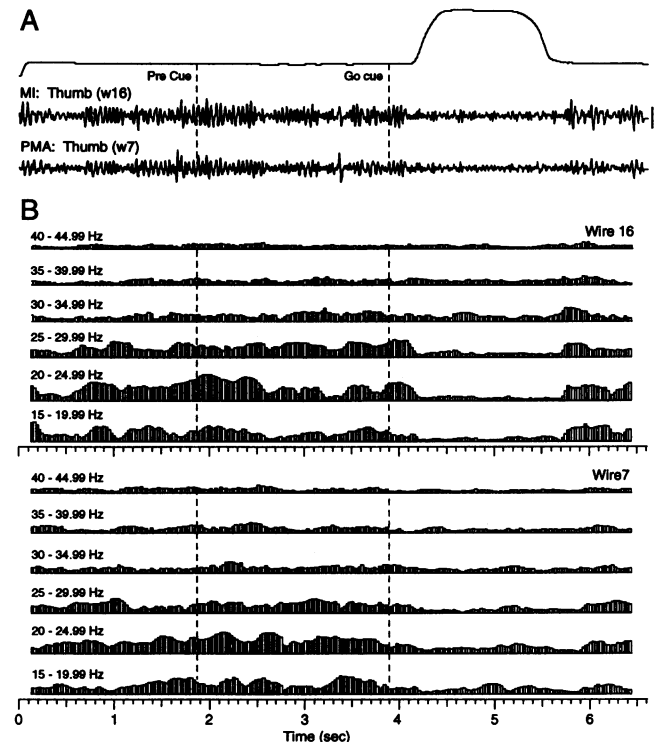


FIG. 3. Frequency characteristics of motor cortex LFPs. (A) Recordings from MI and PMA during a single trial performed by monkey FD. The cued preparatory period occurred between the dashed lines, and go-cue onset is indicated by the rightmost dashed line. (LFP calibration = 100 μ V.) (B) Cumulative amplitude of the Fourier decomposition of the LFP recordings in 5-Hz bandwidths from 15 to 45 Hz calculated in 256-msec epochs and stepped across the trial in 25-msec increments. Note that the power in the three bands from 15 to 30 Hz exhibited the greatest spectral density before movement and the most diminution of power during active movement.

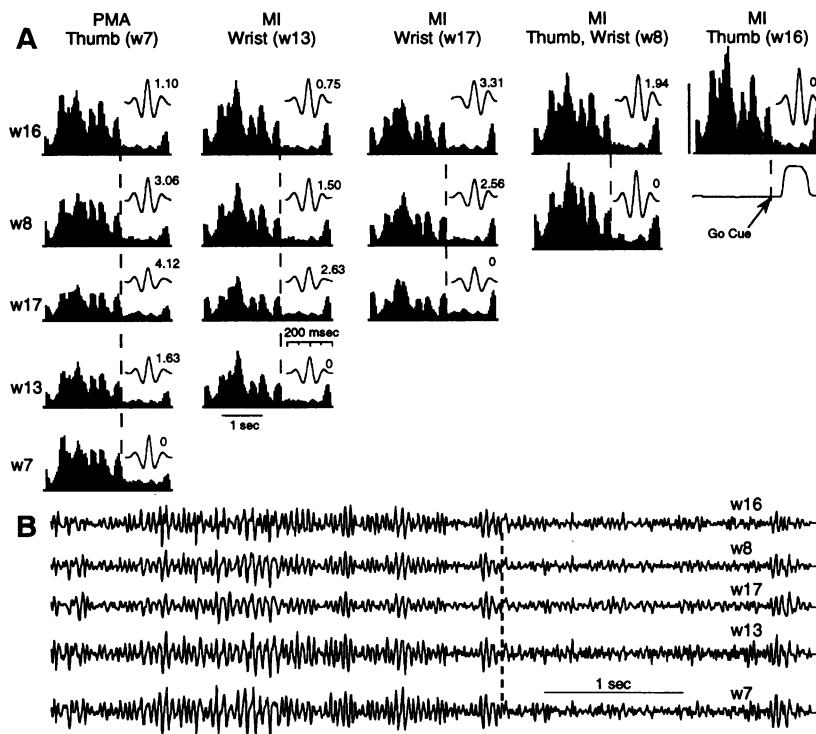


FIG. 4. Interactions between cortical sites. (A) Auto- and cross-correlation matrix of a selected set of LFP recordings during a single wrist movement (displayed under histogram in upper right) performed by monkey FD. (Insets above right sections) The auto- (on matrix diagonal) or cross-correlogram of the recording pairs computed across the entire behavioral trial; only the central portion of these records is shown. Each histogram bin represents the peak value of auto- and cross-correlograms of short epochs across the behavioral trial (see text for details). (Correlogram calibration for entire epoch = 0.05; calibration for sliding correlograms = 0.1.) (B) LFP recordings from each site depicted in A. (LFP calibration = 100 μ V.)

high peak correlations in the hold and pre-cue periods but with significant fluctuations, and decreased correlation at movement onset, reflecting the cessation of the high-amplitude oscillatory activity. Although there was considerable variability in the time of onset and duration of oscillations from trial to trial, the pattern of strong correlation between wire pairs in the hold and pre-cue period was observed across trials (data not shown).

DISCUSSION

These results demonstrate that widespread synchronous oscillatory activity occurs in motor cortex during preparation for visually guided movements. The cessation of oscillatory activity occurs simultaneously across motor cortex at movement onset. Thus, these results confirm prior observations that LFP oscillations occur in motor cortex of behaving monkeys (9) and demonstrate spatiotemporal features of neural oscillatory activity occurring during preparation and performance of learned movements to visual targets. Oscillations occurred predominantly in the uncued (hold) and cued intervals before visual signals instructed hand motor actions. These oscillations were markedly damped after the go cue and during the dynamic phase of movement, although they could continue into the initial part of digit movements.

Across trials and in both monkeys, oscillations in the LFP occurred consistently throughout the hold and pre-cue periods, although the exact pattern of oscillations varied from short bursts (one cycle or ≈ 25 –50 msec) to nearly continuous periods lasting for several seconds. These findings differ from those of Murthy and Fetz (9), who found LFP oscillations in MI occurring in five-cycle bursts and at very low rates (< 1 /sec) when monkeys performed repetitive wrist movements. In the current experiment, monkeys performed a visually guided step-tracking task requiring precise flexion to a defined target, and LFP oscillations appeared frequently and sometimes continuously throughout the period leading up to movement. A potential reason for the discrepancy in the occurrence of LFP oscillations between our experiment and that of Murthy and Fetz (9) may be differences in the conditions directing the monkeys' behavior, the precision of

the tasks, or when oscillatory activity was evaluated. Our experiments used a more complex step-tracking task that included an instructed delay period during which impending target location could be seen by the monkey, whereas the behavioral contingencies of Murthy and Fetz (9) apparently did not always require target visualization. Regardless of these differences both studies find infrequent LFP oscillations during actual performance of overtrained movements.

Our data support earlier findings from cat (8) and monkey (9, 16) that motor cortex LFP oscillations may be related to attentive states. However, we found no readily apparent relationship between the occurrence or duration of LFP oscillations and onset of instruction cues, which would be expected to increase attentiveness. This finding may be related to our inability to measure or to control attentiveness precisely in the hold or pre-cue periods. Nevertheless, short and consistent reaction times suggest that the monkey maintained a high level of attention during the variable-length instructed delay period.

The most notable temporal relationship of LFP oscillations to behavior was the marked desynchronization and amplitude diminution after the go cue occurred. At this time, movement-related unit activity begins in motor cortex (15), and prime mover muscles begin to contract. The current observations suggest a negative correlation between wrist-related muscle or unit activity and LFP oscillations. However, in the digit task, LFP oscillations often continued into the early phases of task performance, a time when both muscles and units would be intensely active (17). Voluntary muscle activation did not by itself completely suppress LFP oscillations because oscillations often reappeared soon after the monkey achieved a static torque required for liquid reinforcement. Thus, LFP oscillations in motor cortex seem not simply related to active movement but to the myriad of processes leading up to generation of phasic muscle activity. They may be related to neurons, termed "set" cells (18), with discharge patterns that modulate during movement preparation (19–21). That oscillations occurred during the initial phases of the digit task and occurred more frequently when monkeys performed tasks requiring skilled digit or wrist manipulation (9) argues against a simple conclusion that only attentional

states drive LFP oscillations. However, the complex relationships between muscle, unit, and LFP activity suggest that LFP oscillations are related to membrane potential fluctuations of only a subset of neurons or perhaps even cortical afferents.

The data recorded in these experiments confirm that synchronous activity between 15 and 50 Hz occurs in primary and nonprimary motor cortical areas. Thus, oscillations appear to be a general and prominent feature of motor, in addition to sensory, cortex in alert animals, although one recent report argues against a prominent role for neural oscillations in information processing (22). Although the frequencies of LFP oscillations obtained in our two macaque monkeys fell within described ranges (2, 3, 9), the dominant LFP oscillation frequency in the two animals diverged by >10 Hz. These differences were evident, even though the monkeys performed under nearly identical stimulus-response conditions. The differences in oscillation frequency may be related to disparities in motor behavior of the two monkeys. Indeed, there was greater stereotypy in the movements performed by monkey FD than those of monkey FC.

We commonly observed robust correlations between paired LFP recordings obtained within and between frontal motor cortical fields. In MI, nearby (<2 mm) and far apart (>5 mm) sites exhibited comparable cross-correlograms, indicating not only did common neural processing occur throughout MI and into PMA but that, contrary to prior observations (9, 23), the strength of interaction did not diminish with intracortical distance within or between cytoarchitectonic fields. Finally, significant interactions occurred between paired LFP recordings in primary and nonprimary motor cortex, and they could be stronger than nearby interactions within the same field. Further investigations of neural activity interactions occurring at paired sites within and between defined cortical areas may provide functional correlates of the known connectivity patterns of motor cortex (24–26).

Our data on intraareal correlations in frontal motor cortex agree with reports of correlated activity between visual cortex areas. Synchrony of LFP oscillations occurs between striate and extrastriate visual cortex (12), and, from our observations, also between primary and nonprimary frontal motor areas. Between visual cortical areas, Engel *et al.* (12) showed that sites with similar receptive field mapping in striate and extrastriate cortex exhibited stronger common oscillatory responses than sites with unrelated receptive fields. In motor cortex, common oscillations occurred between paired sites with similar and different representations of motor actions, as revealed by intracortical electrical stimulation. Because MI sites representing different joints have complex interconnections (26), similarity of electrical stimulation effects might not be a predictor of intersite LFP correlation in MI and PMA. Instead, more complex behavioral properties of motor cortex neurons and a better understanding of motor cortex organization may be more salient than electrical stimulation effects in predicting intersite correlation magnitude.

These studies leave unresolved the nature and source of neural oscillations. Earlier studies suggested that oscillations are correlated with common population neural activity (12). No such simple relationship like this seems to exist in motor cortex, though LFP oscillations occur more frequently during

movement preparation and less so at movement onset when neural activity is high. Nevertheless, LFP oscillations could reflect activity of those motor cortex cells related to movement preparatory or attentive states. The finding that fewer than half the single- or multiple-unit neural recordings in visual cortex have periodic activity (27) reinforces the idea that oscillations may reflect resonance among a select neural sample. This speculation remains to be resolved.

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