Neural Discharge and Local Field Potential Oscillations in Primate Motor Cortex During Voluntary Movements

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Donoghue, John P., Jerome N. Sanes, Nicholas G. Hatsopoulos, and Gyöngyi Gaál. Neural discharge and local field potential oscillations in primate motor cortex during voluntary movements. *J. Neurophysiol.* 79: 159–173, 1998. The role of ''fast,'' or gamma band (20–80 Hz), local field potential (LFP) oscillations in representing neuronal activity and in encoding motor behavior was examined in motor cortex of two alert monkeys. Using chronically implanted microwires, we simultaneously recorded LFPs and single or multiple unit (MU) discharge at a group of sites in the precentral gyrus during trained finger force or reaching movements, during natural reaching and grasping, and during quiet sitting. We evaluated the coupling of oscillations with task-related firing at the same site, the timing of oscillations with respect to the execution of trained and untrained movement, and the temporal synchrony of oscillations across motor cortical sites. LFPs and neural discharge were examined from a total of 16 arm sites (7 sites in 1 monkey and 9 in the other), each showing movement-related discharge modulation and arm microstimulation effects. In the trained tasks, fast LFP and MU oscillations occurred most often during a premovement delay period, ceasing around movement onset. The decrease in oscillation roughly coincided with the appearance of firing rate modulation coupled to the motor action. During this delay, LFP oscillations exhibited either ''overlapping'' or ''mixed'' relationships with the simultaneously recorded neural discharge at that site. Overlap was characterized by coincident epochs of increased neural discharge and LFP oscillations. For the mixed pattern, episodes of LFP oscillation typically coincided with periods of diminished firing but overlap also sometimes appeared. Both patterns occurred concurrently across motor cortex during preparation; LFP suppression with motor action was ubiquitous. Fast oscillations reappeared quickly upon transition from quiet sitting to resumption of task performance, indicating an association with task engagement, rather than the general motor inaction of the delay period. In contrast to trained movements, fast oscillations often appeared along with movement during untrained reaching, but oscillations occurred erratically and were not reliably correlated with elevated neural discharge. Synchronous oscillations occurred at sites as much as 5 mm apart, suggesting widespread coupling of neurons and LFP signals in motor cortex. Widespread coupling of oscillatory signals is consistent with the concept that temporal coding processes operate in motor cortex. However, because the relationship between neuronal discharge and the appearance of fast oscillations may be altered by behavioral condition, they must reflect a global process active in conjunction with motor planning or preparatory functions, but not details of motor action encoded in neuronal firing rate.

INTRODUCTION

Skilled voluntary movements appear to rely on signals derived from a broad region of the cerebral cortex to produce highly coordinated interactions among sets of muscles. To varying extents, a collection of motor cortical areas contribute to preparing and performing skilled voluntary movements. It remains unclear how information is organized across and within motor cortical fields into a coherent output that directs complex motor actions, although motor signals appear to emerge from the concerted interaction of large populations of neurons (Georgopoulos et al. 1993). Recently it has been proposed that temporal conjunctions among populations of visual cortical neurons, a process often termed ''binding,'' provides a mechanism for feature association and other forms of higher level cortical representations (Crick and Koch 1990; Eckhorn et al. 1988; Engel et al. 1991; Gray and Singer 1989; von der Malsburg and Schneider 1986). Fast oscillations, those in the beta to gamma range (~15–90 Hz), have generated considerable interest because they may reflect binding of cortical cell assemblies. The presence of oscillations in motor cortex could be a marker of neural assembly formation related to representation and association of movement features, such as the coordination of direction, velocity, and force or to the formation of muscle groupings used in a skilled action (Jeannerod 1994).

Fast oscillations have been described widely within the cerebral neocortex based on recordings of local field potentials (LFP) and, to a lesser extent, neuronal firing (see Gray 1994 for a review; also Livingstone 1996). The relationship between cortical LFP oscillations and neural discharge is central to understanding the type of information carried by oscillations. On the basis of recordings made largely in visual cortical areas of anesthetized animals, LFP oscillations appeared to correspond to the collective discharge of local neuronal clusters (Gray 1994). In support of this view, neuronal firing in visual cortex correlates with the phase and amplitude of LFP oscillations and LFP signals can show orientation tuning similar to that of nearby neurons (Gray and Singer 1989). However, LFP oscillations also can be distinct from nearby neuronal firing evoked by visual stimuli (Eckhorn and Obermueller 1993; Gray 1994; Livingstone 1996). Observations in the primary motor cortex (MI) further reveal a complex LFP-neural discharge relationship. In MI, LFP oscillations most often occur before movement onset and are much less evident during motor actions (Lado et al. 1991; Murthy and Fetz 1996a,b; Rougeul et al. 1979; Sanes and Donoghue 1993) despite the fact that a large proportion of MI neurons only begin to modulate their discharge near movement onset (Evarts 1981). Therefore it would appear that during times of highest neuronal activity in MI, LFP oscillations diminish substantially, making a tight coupling with movement-related neuronal firing implausible. This temporal arrangement also appears to conflict

with a role for oscillations in binding processes involved in motor performance, which would predict the emergence of oscillations during movement-related discharge. Although many MI neurons discharge just before and during motor action, other patterns exist (see, e.g., Johnson et al. 1996) that may correlate with premovement LFP oscillation patterns. The correspondence between neuronal firing patterns and LFP oscillations at sites having separate preparatory and movement periods has not been described. Thus one goal of these experiments was to test the hypothesis that LFP oscillations accurately reflect the firing of nearby neurons by comparing the two signals at a collection of sites showing movement-related discharge modulation.

The fact that oscillations precede certain motor actions suggests a role in movement planning or preparation rather than the details of motor performance. Numerous studies have found a better correlation of oscillations to periods in advance of movement rather than to their actual performance (Bouyer et al. 1987; Kristeva et al. 1991; Lado et al. 1991; Llinás and Ribary 1993; Murthy and Fetz 1992; Pfurtscheller and Neuper 1992; Rougeul et al. 1979; Samelin and Hari 1994; Sanes and Donoghue 1993). For example, LFP oscillations in cat MI occur during motionless episodes that appear to be periods of focused attention; these oscillations are disrupted by self-initiated movements (Bouyer et al. 1987). Further, as noted above, fast LFP oscillations recorded in monkey motor cortex during operantly conditioned step-tracking tasks appear primarily during a required premovement waiting period and decrease abruptly after a visual cue to move (Sanes and Donoghue 1993). Such observations suggest that oscillations before motor action could reflect planning or more global signals related to an upcoming behavior or they could simply reflect relative inactivity of motor cortex neurons until close to the time of motor action. Concurrent LFP and neural discharge oscillations during untrained exploratory grasping movements in monkeys (Murthy and Fetz 1992, 1996) and fast oscillations in human electroencephalogram recordings during, as well as before, self-paced button pressing (Pfurtscheller and Neuper 1992) suggest that fast oscillations more likely are related to an active process. However, for MI it is not clear whether they are related to ongoing motor cortical activity required for performing precise, self-directed movements or are related to aspects of motor planning or preparation that occur in advance of movement, if planning time is allowed, but occur during movement if planning and performance occur together. Thus a second goal of the present studies was to investigate the relationship of oscillations to motor planning and performance.

Our approach in these studies was to examine simultaneously recorded LFP oscillations and neural discharge at sites associated with arm motor actions on the basis of neural discharge patterns and electrical stimulation effects. Using chronically implanted microelectrodes, we compared activity patterns at the same sites during motor actions of the fingers or arm that allowed ample time for motor preparation, during untrained reach and grasp movements to hidden goals and during periods of inactivity with maintained alertness. If oscillations were related to a global planning process, they should occur largely when ample time is allowed for preparation and during motor actions when preparation and performance occur simultaneously. Finally, if oscillations signify a process necessary to motor behavior, they should diminish with quiet sitting and should emerge when task engagement begins.

Our third goal was to begin to examine the temporal synchrony of LFP and neural discharge across MI to determine whether synchrony could be used for encoding of motor-related processes. We used cross-correlation methods to evaluate the occurrence of synchronous activity across the set of simultaneously recorded motor cortical sites. If binding is a general cortical operation, we expected to detect temporal synchrony in motor cortex similar to that found in visual cortex. Portions of these data have been presented previously in abstract form (Gaál et al. 1992).

METHODS

Behavioral apparatus and tasks

Simultaneous field potential and single or multiple unit (MU) recordings were made in two *Macaca fascicularis* monkeys (*FC* and *FD*) trained to perform voluntary motor actions. Four behavioral conditions were used. For the first, both monkeys were trained to perform a step-tracking, finger force task. Flexion directed finger force was transduced by a strain gauge (Grass Instruments, Model FTO3) covered with a plastic plate. The plate and strain gauge had a stiffness of 8 g/mm. A 27 × 34 cm black-and-white monitor (black background), placed 36 cm from the monkey, presented video images for behavioral control. This task required a period of premovement waiting followed by production of a specific finger flexion force after the appearance of a ''go-cue'' to receive fluid reinforcement. Each monkey typically held digits 2 and 3 on the plate in a stereotypic manner while performing the task, although it could be performed with any or all of digits 2–5. A video monitor provided visual instructions by displaying cursors representing finger force and target locations. A visual precue signaled the target amplitude of the impending motor action and a separate cursor that moved horizontally provided feedback proportional to force. To perform the task, monkeys initially maintained alignment in a ''neutral'' hold zone requiring <0.02 N finger flexion (downward) force for a 1.5–2.5 s hold period. At the expiration of the hold period, the precue (a dashed-line box) appeared on the video monitor. This precue signaled an impending go-cue and visually identified the force target required for the upcoming motor action. After a 2–3 s delay (preparatory period), a go-cue appeared (transformation of the broken-lined, precue box into a solid-line box at the same location). Hold and preparatory times were varied pseudorandomly. The trial restarted if the monkey increased force before appearance of the go-cue. The monkey received liquid reinforcement if it successfully realigned the force cursor with the new target location (requiring 0.16 N) within 1 s and then maintained the target force for 0.5–1 s.

Monkey FD was trained in a second task that required planar reaching movements of 6 cm to one of three targets (three-direction task). Arm movements originated from a hold zone centered at the body midline and terminated at one of three perpendicularly arranged locations (left, away, or right). To perform this task, the monkey grasped a handle that was attached to a two-link mechanical arm. The device permitted horizontal motion across the surface of a digitizing tablet. A sensor in the handle reported hand position on a video monitor, with a 1:1 ratio of cursor movement to hand excursion. During task performance, the monkey was required to align the position feedback cursor at a central hold position for 0.8–1.8 s (hold period), after which a movement target appeared randomly at one of the three target locations. After an additional 2 s of steady holding (preparatory delay), the movement target

changed appearance from an unfilled to a filled (white) circle appearing on a black background. This signal served as a go-cue. If movement to the target was completed within 0.8 s and the target zone held for 0.5 s, liquid reinforcement was delivered.

For a third behavioral condition, recordings were made during self-initiated periods of quiet sitting between episodes of performing the finger force task (2 in *FC*, 1 in *FD*). Data obtained when the monkey stopped performing the finger force task, sat quietly for ~5 min, and then returned to task performance were used for analysis. In the final behavioral condition, recordings were made twice at a set of arm related sites in *FC* during untrained exploratory reaching and grasping. The monkey reached with the right arm to obtain food morsels (Fruit Loops cereal) placed out of view in a bowl that was held in various locations in front of the monkey. This action required object manipulation and initial grasp of the food using the fingers without direct visual guidance. A single axis accelerometer (Grass Instruments, model SPA1) aligned coaxially with the second metacarpal bone was taped to the dorsum of the hand to provide crude information about the reaching and grasping.

Cortical wire implantation

Before surgery both monkeys were trained to perform a wrist flexion task unrelated to the present study (see Sanes and Donoghue 1993) to a criterion of 90% correct performance. Next, microwires were implanted chronically into the frontal motor cortex. For each surgery, monkeys initially were anesthetized with ketamine injection (10 mg/kg im), then the surgical field was shaved and washed with betadine. After tracheal intubation, surgical levels of anesthesia were obtained using Isoflurane vapor in 100% O_2. An intravenous line was inserted in the saphenous vein to deliver fluids and electrolytes. The electrocardiogram, respiratory CO_2, and body temperature were monitored continuously throughout all surgical procedures. The monkey was mounted in a stereotaxic frame and the frontal motor cortex was exposed by craniotomy. Then a connector and wire assembly with 24 PtIr wires (A-M Systems, Teflon-coated 90% Pt, 10% Ir wire, 7760; 51 μm bare, 76 μm coated) plus two ground wires (A-M Systems, Pt rod 7110; 250 μm diam) was fixed to the skull using anchoring screws and dental acrylic. The exposed dura mater was incised and removed, after which a digital video image of the cortical surface was taken. Sulcal landmarks appearing on the video image were used to localize the general region of MI and nonprimary regions of the frontal motor cortex and to mark the location of wire insertion (see Fig. 1). Wires were inserted into the cortex by grasping them with smoothed, plastic-coated forceps attached to a precision stereotaxic manipulator. Each wire from the assembly was inserted into the cortex to a depth consistent with layer V at the insertion site: ~2-mm deep on the flattened areas of the precentral gyrus and from 2- to 6-mm deep when inserting into the depths of the posterior bank of the gyrus. After insertion of all microwires and placement of ground wires onto the cortical or nearby dural surface, a fibrin tissue adhesive compound (Tisseal, kindly donated by Immuno US) was spread over the cortical surface to cover the defect. The entire assembly then was enclosed with dental acrylic. For this experiment, neural recordings were obtained from *monkey FC* 14 mo after surgery and 4 mo after surgery in *monkey FD.*

Data recording and intracortical stimulation

Intracortical electrical stimulation was used to characterize electrode implantation sites using pulse trains (333-Hz, 30-ms duration, 200-μs pulses; WP Instruments Stimulator Model 1803-1803A) at currents $\leq$60 μA. We noted movements evoked by threshold and suprathreshold stimulation at each site, and these data were used to identify wires located in the motor cortex upper limb area (Fig. 1).

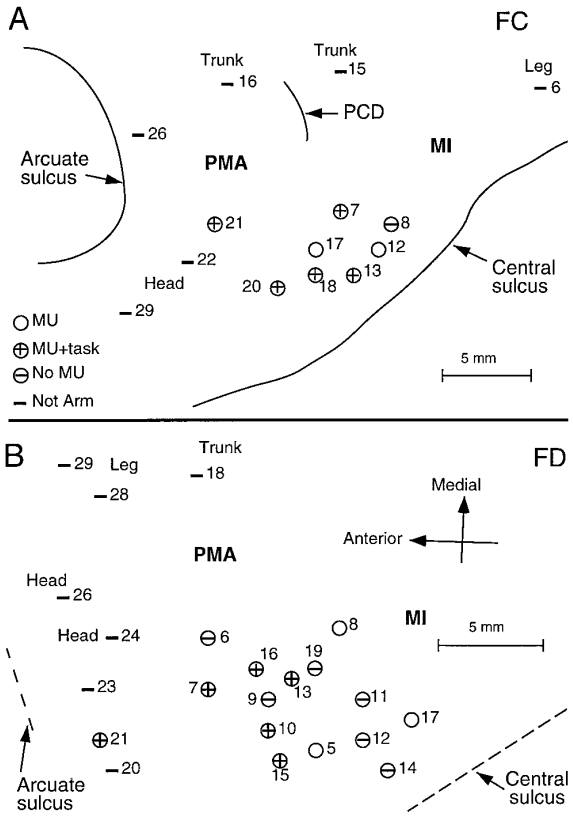

FIG. 1. Microwire insertion and recording sites. *A*: *monkey FC; B*: *monkey FD.* On these surface views, each symbol represents an insertion site; wire number for that site is placed nearby. ○, sites where multiple unit (MU) activity exhibited modulation during the finger force task. ⊕, recording sites also used for untrained reach and grasp movements in *A* and sites showing MU modulation during the 3 direction reaching task in *B.* ⊖, arm stimulation sites where units could not be recorded. At the remaining locations, stimulation evoked movements of other body parts are marked by general region: —, head, leg, or trunk. MI, primary motor cortex; PMA, region of premotor area; PCD, precentral dimple. – – –, *B* mark approximate location of the arcuate and central sulcus, which are more tentatively placed because they could not be viewed definitively on the image of the cortical surface taken at surgery.

For cortical recordings, a miniature multichannel preamplifier (Microprobe) was attached to the connector on the monkey's head, and the preamplifier cable was led to a 16-channel Grass Instruments amplifier system (Neurodata 12). Electrical activity was recorded simultaneously from a subset of microwires of interest. Filtering was set to a broadband between 10 Hz and 3 kHz, with 5,000 $\times$ amplification, for later differentiation of MU activity and LFPs. These broadband signals were stored on a 16-channel PCM videotape system (Vetter Instruments, Model 4000A, rise time 200 μs/channel). Other signals related to the trials, including finger force and computer-generated event codes signaling start of trial, precue, go-cue, movement onset, and reward also were recorded on tape; hand position (reaching task) was recorded to disk at 100 Hz using a Macintosh computer.

Data processing

Tape recorded neural signals were processed off-line for LFP and MU analysis using Datawave software on a PC and Igor software (Wavemetrics) implemented on Macintosh computers. Epochs starting from the beginning of the hold period and lasting

until 1–2 s after reward delivery (total time 4–7.5 s) were filtered (LFP = 10–100 Hz; neural discharge = 0.3–3 kHz) and digitally sampled at 10 kHz/channel. The LFP (500 Hz), force and event (167 Hz) records were down-sampled digitally. A 10–100 Hz digital filter was applied to the LFP before further quantification.

Action potential occurrences (spike times) for discriminable spikes were based on amplitude, waveform slope, and event duration using Datawave software (V3.1, 4.0). To obtain spike times in MU unit records, a discriminator threshold for positive slope detection was set to about twice background noise. Spike time files were used to create event histograms and correlograms. Cross- and autocorrelations were performed to establish relationships between spike occurrence and LFP oscillations. For correlation analyses of discriminated neural discharge data, the discrete spike-time data files were transformed into a continuous spike density function by convolving each timing pulse in the series with a Gaussian pulse-time function (SD: 2 or 10 ms) (Richmond et al. 1987). This procedure transforms the binary spike time record into a continuous waveform resembling the instantaneous discharge rate. Cross-correlogram functions were calculated between this resulting spike density waveform and the concomitantly recorded LFP waveform. Autocorrelograms for single trials were also calculated from spike density functions, and cross-correlograms were computed for pairs of MU spike density functions using Igor or Datawave software.

Histology

At the termination of the experiments, one monkey (*FC*) was perfused with saline followed by 10% formol saline. The brain was fixed further and then parasagittal sections made through the frontal cortex were stained with thionin to identify recording sites. No histological material is available from the second monkey because it continues to participate in experiments.

RESULTS

Recording sites

Among the 36 insertion sites in the two monkeys, 16 were identified as precentral arm movement-related sites suitable for further analysis. This selection was based on electrical stimulation effects and neural discharge modulation in the finger force task. Figure 1 illustrates a surface view depicting arm sites among the 36 wire insertions in the two monkeys. Electrical stimulation at 9 of 14 sites in *FC* and 17 of 22 sites in *FD* evoked arm movements (Fig. 1, ○, ⊕, and ⊖). Wrist and digit movements were the most commonly evoked movements at threshold currents at the arm sites; more proximal movements, including shoulder movements, were elicited at 10 of 13 digit sites at intensities 2–15 μA higher (mean = 5.1 μA). From these 26 arm sites, recordings at 16 (7 from *FC*, 9 from *FD*, Table 1) revealed MU discharge associated with finger force actions (circled sites in Fig. 1). These 16 task modulated ''arm'' sites formed the data set used for all subsequent analyses and comparisons. The remaining sites showed either no indication of resolvable neural discharge or no task modulation of neurons recorded at that site (see Fig. 1); such sites therefore were eliminated from further analysis. With two exceptions, recordings filtered for neural discharge were composed of MU clusters. Firing patterns and signal to noise ratios varied from site to site (see examples in Figs. 4–6 and 9) but were generally similar for a particular site over many days of recording. Signal-to-noise ratios were generally higher in *FC* than in *FD*, although single cells could be well-isolated at two sites in *FD*. Within the complete set of 16 arm sites, MU activity patterns revealed in raster-histogram displays resembled those commonly observed for single neurons in motor cortex (Figs. 2 and 3) (e.g., Evarts 1981). These patterns included both phasic and sustained increases or decreases in discharge around the onset of motor action. Based on this collection of features, the posterior most sites fall within MI. More rostral sites may be located in premotor areas (areas 6), but because electrode tracts were not evident in the histological sections available from *monkey FC* and no histology has been performed on *monkey FD*, a more precise localization

TABLE 1. *Characteristics of cortical recording sites in monkeys FC and FD*

		Electrical Stimulation Effects				
Animal	Wire	Evoked Movement at Threshold	Current, μA	LFP Peak Frequency, Hz*	Peak Unit Oscillatory Frequency, Hz	LFP/MU Relationship (Finger Force Task)
FC	7	W ext	5	38	42	Overlap
	12	D1 flex	12	38	40	Mixed
	13	D1 ext	3	39	40	Overlap
	17	D1 ext	2	30	40	Mixed
	18	D2 ab	6	34	48	Mixed
	20	D2 ext	4	34	48	Mixed
	21	D1 ext	2	34	38	Overlap
FD	5	D1 ad	13	18	17	Mixed
	7†	D1 flex	11	17	17	Mixed
	8	D3 ext	7	18	11	Mixed
	10**	Wr ulnar dev	13	26	17	Overlap
	13**	D3 ext	11	21	17	Overlap
	15**	D1 Flex	34	24	17	Overlap
	16**	D2,3 flex	6	22	18	Mixed
	17	W ext	20	21	17	Mixed
	21**	D2-4 flex	20	19	16	Mixed

Overlap, periods of prominent local field potential (LFP) oscillations corresponded to periods of elevated multiple unit (MU) discharge. Mixed, periods of prominent oscillations mainly occurred during epochs of lower neural discharge during the trial, although some overlap also occurred. ext, extension; flex, flexion; sup, supination; ab, abduction; ad, adduction. * Based on recordings during the finger force task. † Also recorded in three direction reaching task.

of these sites is not possible. As summarized in Table 1, seven sites considered to be arm area sites in *monkey FC* (Fig. 1*A*), whereas there were nine such sites in *FD* (Fig. 1B).

LFP oscillations during finger force task

Episodes of LFP oscillation, defined as large-amplitude cyclical waves, were evident at all 16 task-modulated arm sites. We previously have characterized LFP oscillations obtained from earlier recordings from *monkeys FC* and *FD* during wrist flexion and finger force tasks (Sanes and Donoghue 1993). Therefore, aside from a brief description of the main characteristics of the LFP obtained during this task, only aspects of LFP oscillations relevant to comparisons with neural discharge or to the set of behavioral tasks are presented. As reported previously (Sanes and Donoghue 1993), LFP oscillations had a characteristic relationship to task period across all sites. They occurred primarily in the hold and preparatory intervals of instructed delay tasks (Fig. 3–6, 9, and 10). Often similar episodes were evident concurrently across multiple sites, although they varied in their detail at each site (e.g., compare oscillations at the 5 sites for the single trial shown in Fig. 4). LFP oscillations cease either just before or during the dynamic phases of the motor

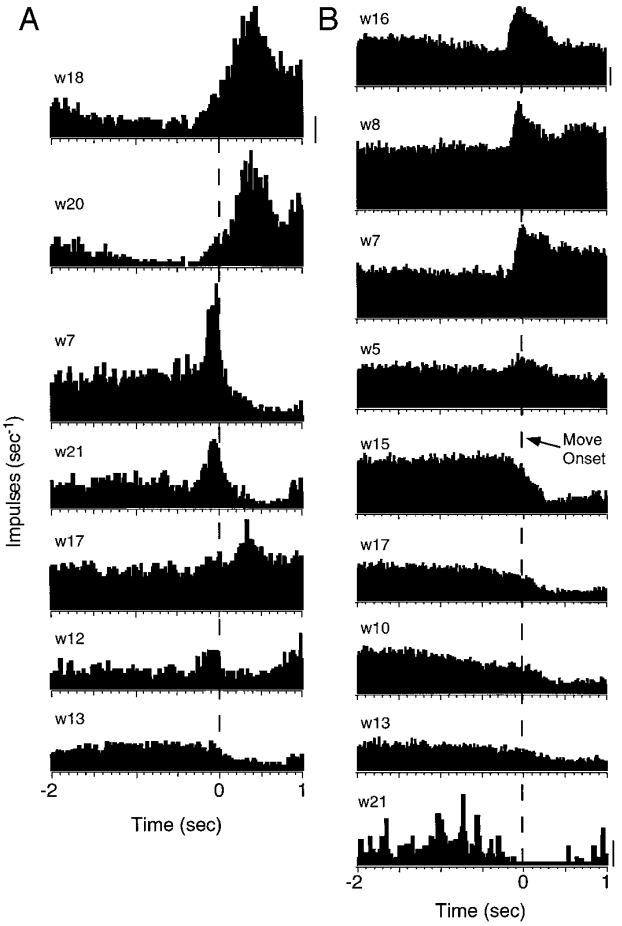

FIG. 2. Task-related neural activity during the finger force task. Event histograms compiled from MU activity during the isometric finger force task are shown for *monkey FC* (*A*, 60 trials) and *FD* (*B*, 40 trials). Each histogram was aligned on finger force onset (*time 0*, – – –). Histograms are ordered according to the prominence of the phasic increase of activity associated with motor action to permit comparison with correlograms in Fig. 7. Calibration bar *A* = 20 impulses/s, *B* = 50 impulses/s; bar next to wire 21 in *B* applies to that histogram only.

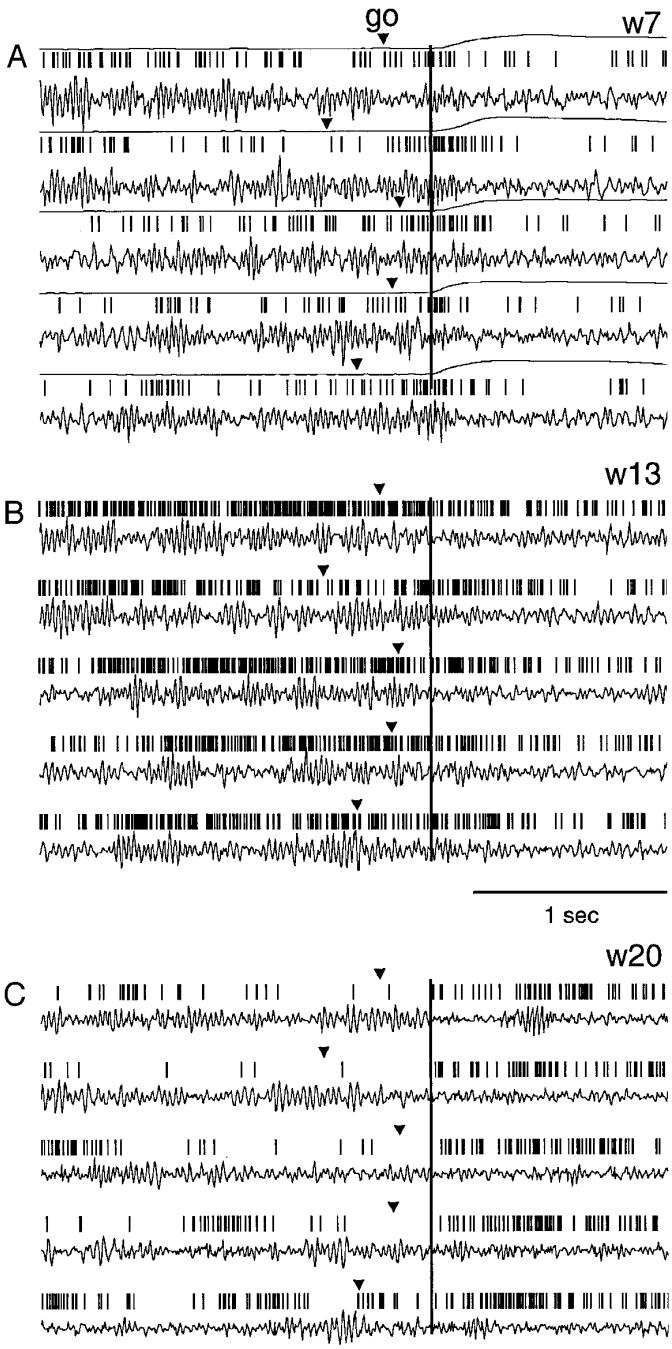

FIG. 3. Consistency of local field potential (LFP) oscillations and neural discharge modulation across 5 successive trials in the finger force task at 3 simultaneously recorded sites in *monkey FC* (*first trial* at *top*). Each panel illustrates force record (*top line*), window discriminated MU discharge (vertical marks), and LFP (*bottom*) for 5 trials (*A*, wire 7; *B*, wire 13; *C*, wire 20). ▼, time of the go-cue; alignment is for onset of finger force (solid vertical line). LFP oscillations occur primarily during hold or preparation and, with some variability, in the earliest phases of the motor action. Note that although MU discharge occurs consistently around movement onset, prominent fast LFP oscillations may (*A, trials 2* and *5*, just after movement onset) or may not (*A, trial 4*) accompany this neuronal firing.

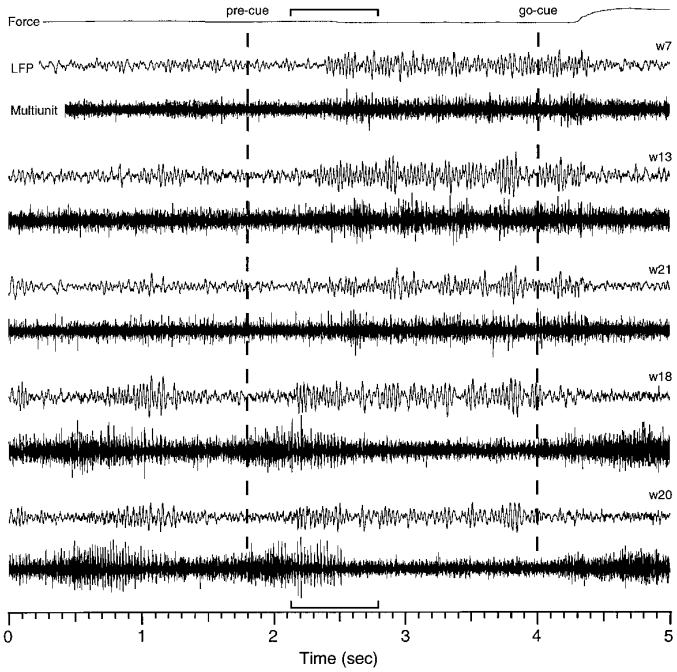

FIG. 4. Overlapping and mixed relationships of LFP oscillation and neural discharge. Illustrated are the finger force (*top*) and pairs of LFP and MU filtered records from each of 5 simultaneously recorded sites (7, 13, 18, 20, and 21, *monkey FC*). *Time 0* indicates onset of hold period. Two relationships are evident among subsets of sites: 1st, LFP oscillations and epochs of higher MU activity tend to overlap for wires 7, 13, and 21; 2nd, the 2 activities are mostly reciprocal for wires 18 and 20, except for a period of repetitive MU discharge, which coincides with LFP oscillations for ~500 ms (bracketed region). Note that activity of the largest amplitude neurons ceases while the LFP oscillations continue until motor action ensues. Data are shown at higher temporal resolution in Fig. 5.

action, but during this phase, there is considerable trial-to-trial and intersite variability. These features are evident in Fig. 3, which shows LFP records from three simultaneously recorded sites during five successive trials. This figure also illustrates the prevalence of LFP oscillations before action, their general absence during sustained finger force, and the substantial overall trial-to-trial variability in their features. Trials for wire 7 (Fig. 3*A*) illustrate how oscillations may (*trials 2* and *5*) or may not (*trial 4*) occur during the episode of elevated discharge that accompanies the onset of motor action. To document changes in oscillation with task period, we compared the integral of the ''fast'' range of the power spectrum (20–60 Hz) in 500-ms epochs before and after movement onset, as well as before and after the precue for six sites. At each site, there was a marked decrease in the fast range of the spectrum after movement onset ($P < 0.005$, one-tailed *t*-test) to 58 ± 5.7% (mean ± SD) of the premovement value (range 49–64%). Oscillations do not appear to provide a strong distinction between the hold and preparatory periods, but differences were significant at some sites. In four of the six sites evaluated, there was a small increase in power (17 ± 2.04%; range 3–41%) after the preparatory period began ($P < 0.05$), suggesting that there was some influence of the appearance of the movement instruction on the occurrence fast oscillations.

LFP oscillations sometimes lasted only briefly (Fig. 3), but at other times or at different locations they persisted for several seconds (Fig. 4). No evident relationship emerged between the duration of LFP oscillatory episodes and finger force task performance; both short and long oscillatory episodes were observed in the LFP recordings obtained simultaneously at different motor cortex sites (Fig. 3, *B* and *C*). Peak frequencies of LFP signals in *FD*, (ranging from 19 to 29 Hz) were generally lower, but overlapped those in FC (range: 28–40 Hz, Fig. 7, Table 1) (also see Sanes and Donoghue 1993). Because LFP signals in the frequency range of 15–80 Hz for *FC* and *FD* were similar in form, as well as in unit and behavioral relationships (as described below), they were considered to be manifestations of fast oscillations in both monkeys.

Relationship of LFP oscillations to neural discharge during finger force task

Simultaneous recordings of the LFP and neural discharge at arm sites revealed a variety of relationships between these two signals. Unit-LFP relationships varied from site to site and were distinctively different when the premovement and the motor action periods were compared. Figure 3 shows LFP signals and the simultaneously recorded neural discharge for three sites selected because they illustrate differ-

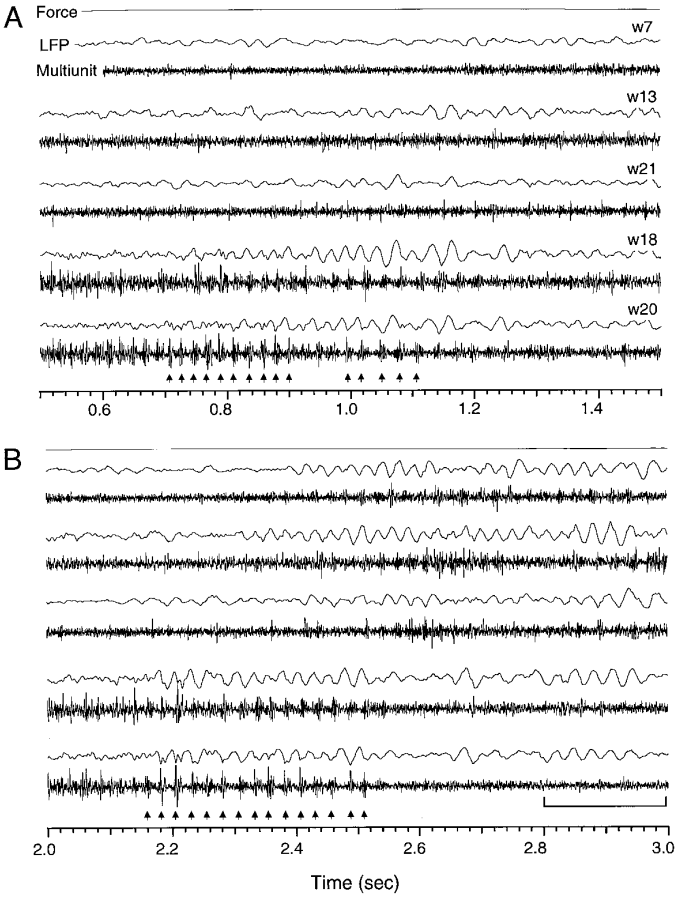

FIG. 5. Selected expansion of 2 time periods in Fig. 4 showing the relationship of MU cluster discharge and LFP oscillations. *A*: hold period (0.5–1.5 s); *B*: preparatory periods (2–3 s). Examples of periodic bursting in the MU record are indicated (↑). Note in particular the coincidence of LFP oscillations and repetitive MU discharge for the overlap period in wires 18 and 20 (*B, bottom,* marked by ↑).

ent neural discharge patterns: a phasic increase coupled to the onset of motor action (Fig. 3*A*), a decrease around action onset (Fig. 3*B*), and a tonic increase after its onset (Fig. 3*C*). Despite distinctive neural modulation patterns at each site, LFP oscillations at all sites followed the characteristic pattern of cessation near the beginning of motor activity. During sustained finger force, LFP oscillations were infrequent even when neural discharge was demonstrably elevated (Fig. 3*C*). The correlation between the occurrence of LFP oscillations and the level of neural discharge was most variable at motor action onset. As can be seen in Fig. 3*A*, a discharge increase associated with the onset of finger force for each trial was associated with LFP oscillation on *trials 2* and *5* but not on *trials 3* and *4.*

During the hold and preparatory delay periods, neural discharge and LFP oscillations exhibited one of two broad types of relationships (Fig. 4). The *overlapping* type was distinguished by occurrences of prominent LFP oscillations that roughly coincided with periods of increased MU activity, provided broad spans of activity were considered (Fig. 4, wires 7, 13, and 21). Overlap occurred most commonly in recordings from sites in which MU discharge decreased upon motor action (3/3 sites in *FC*, 3/6 in *FD;* see histograms in Fig. 2). Overlap of elevated MU activity and LFP oscillations was observed in 51 of 56 (91%) successive trials examined from wire 13; the remaining five trials in that series had complex relationships among the recordings that could not be readily categorized. Thus the presence of LFP oscillations at these sites generally predicted elevated MU discharge during premovement delays and was unique to this interval.

A second, mixed pattern occurred during the delay period before motor action at a separate set of sites. This pattern was largely characterized by reduced MU discharge concomitant with episodes of prominent LFP oscillation at that site. Thus the relationship of the two signals at these sites was nearly reciprocal in nature (Fig. 4, wires 18 and 20). However, overlap of the two signals in various forms was evident at mixed sites. One noteworthy pattern was the overlap of the two signals for a few hundred milliseconds, as indicated by the bracketed region in Fig. 4, that was followed by a reciprocal period. This specific pattern was evident in 51 of 87 (58.6%) successfully performed trials examined from wire 20; it was intermixed more irregularly in the other 36 trials, although the epi-

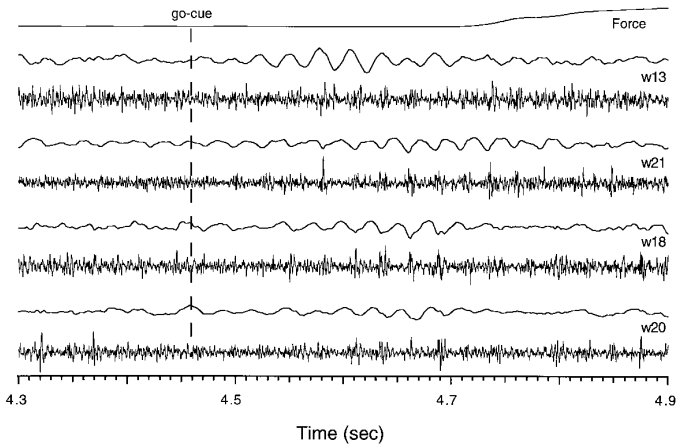

FIG. 6. Example of LFP and neural discharge at 4 simultaneously recorded sites during a single trial of the finger force task. This trial was selected to illustrate periodic MU discharge and LFP oscillations in the interval between the go-cue and force onset. (*Monkey FC,* different trial than shown in Figs. 4 and 5.) Format as for Fig. 4.

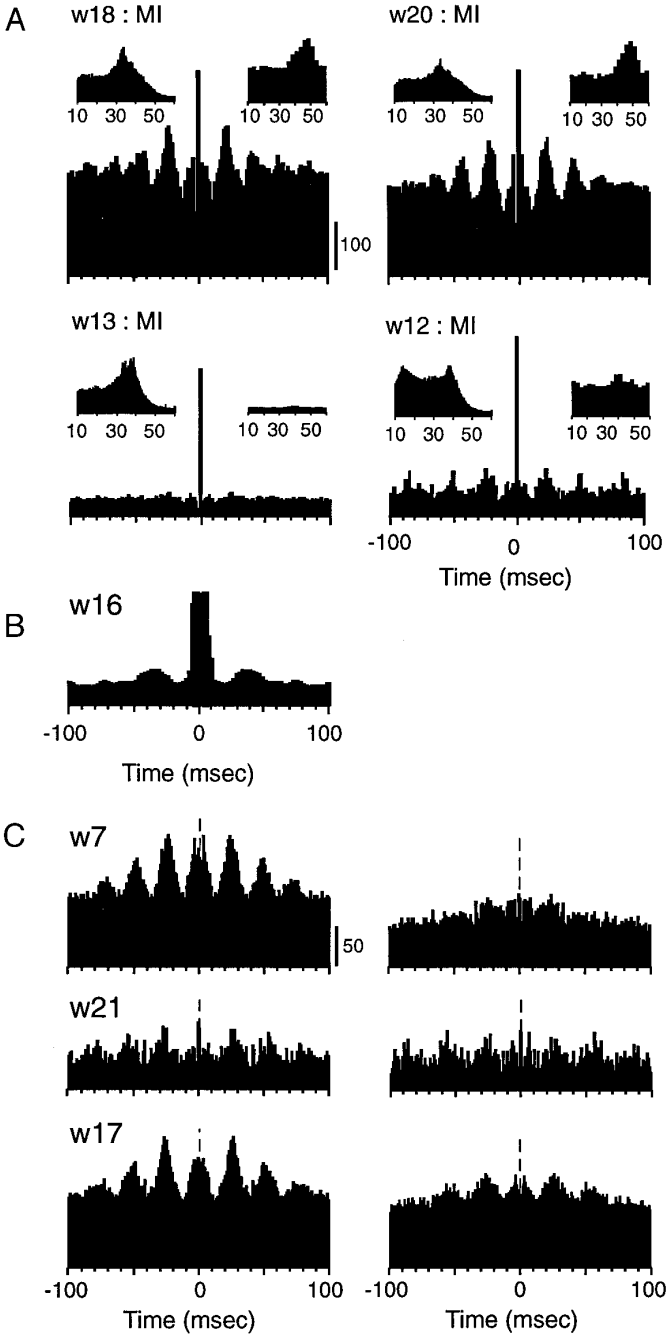

FIG. 7. Periodicity and relationships of LFP activity and neural discharge. *A*: fast oscillation in *monkey FC.* Autocorrelograms (ACGs) are illustrated in the center of each cluster of 3 graphs for each arm site. *Insets* above each ACG show the power spectrum for the simultaneously recorded LFP (*top left*) and MU records (*top right*). Prominent multiple ACG sidebands indicate the oscillatory nature of the MU discharge. A range of oscillation strengths can be seen. *B*: example of MU ACG from *FD.* Data obtained during the finger force task. *C*: decrease in periodic discharge with movement onset. *Left*: ACGs compiled from the preparatory period during the finger force task; *right*: ACGs compiled during after movement onset for the same trials.

sodes of distinct LFP oscillations without firing were consistently evident. This mixed LFP-discharge relationship during the delay period occurred most commonly at sites exhibiting elevated MU activity on finger force action. *FC* had 4 of 7 and *FD* had 6 of 9 mixed sites (Table 1).

Temporal structure of MU discharge

Figures 5 and 6 show more detail of MU firing patterns, and their association with LFP oscillations during holding (Fig. 5*A*), preparation (Fig. 5*B*), and action (Fig. 6) periods of the finger force task. Both periodic and aperiodic MU discharge occurred at overlapping and at mixed sites during single trials. Repeated activation of single cells or MU clusters for three or more times at regular intervals of ~25 ms (Fig. 5, ↑) defined ''periodic'' discharge for the purposes of description. Periodic neural discharge was typically accompanied by LFP oscillations at that site (~0.8–1.0 s in Fig. 5*A;* ~2.2–2.4 s in Fig. 5*B;* ~4.5–4.7 s in Fig. 6). The converse was not necessarily true: as noted above, LFP oscillations occurred in the absence of notable MU discharge, a defining characteristic of mixed type sites (Figs. 4 and 5*B*, bracketed period, ~2.8–3 s). Further, MU discharge lacking distinct periodic structure also could occur during LFP oscillations, as can be seen for wire 13 in Figs. 4 and 5*B* (between 2.6 and 2.8 s).

To verify the occurrence of fast periodic neural discharge, autocorrelograms (ACG) and power spectra were generated from MU recordings obtained during the finger force task from the entire trial or from small trial segments (Fig. 7). The presence of multiple sidebands in the ACG and peaks in power spectra in 10 of 16 task-modulated sites examined in the two monkeys were indicative of fast oscillatory discharge in motor cortex. Sidebands in the ACG ranged from prominent (Fig. 7, *A*, wires 18 and 20, and *B*) to barely or not detectable (Fig. 7*A*, wire 13). Spectral frequencies for MU discharge across the set of 16 task modulated sites were distributed broadly (Table 1). In *FC*, there was substantial spectral power between 25 and 50 Hz (Fig. 7*A*, *insets*), with peak frequencies between 38 and 48 Hz. Spectral frequencies were similarly broad for FD, but peak frequencies were lower (16–18 Hz), as for LFP oscillations. Of note, but currently unexplained, is that the prominence of ACG sidebands occurred in rough proportion to the distinctness of phasic peaks in the event histogram (compare Fig. 2, *left*, and Fig. 7). This finding could suggest the existence of a subclass of neurons that oscillate and are involved in motor action. There was no reliable relationship between threshold currents required to evoke movement and occurrence of MU oscillations; they were seen at high-threshold sites, and some low-threshold sites failed to show clear evidence of oscillation (compare Table 1 with data in Fig. 7).

Similar to LFP oscillations, periodic neural discharge most commonly occurred prior to finger force action (Figs. 3, 4, and 5*B*) and was less evident after force onset (Figs. 3*A* and 6), despite high MU discharge rates for some sites at this time. The shift from periodic discharge with holding to aperiodic discharge during motor action itself is evident in ACGs (Fig. 7*C*). We found no evident time locking of periodic MU activity with any monitored behavioral events such as visual cues or movement onset.

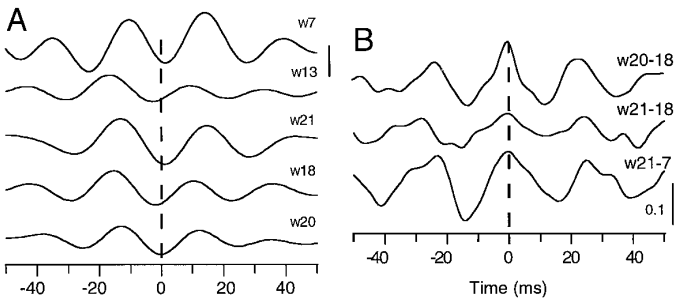

FIG. 8. Timing correlations of neural discharge and LFP oscillations. *A*: cross-correlogram (CCG) between MU spike density functions and concomitantly recorded LFPs at 5 sites (*monkey FC*). Spike data were Gaussian filtered using a standard deviation 10 ms. Note minima in CCGs near *time 0*, indicative of neuronal firing at LFP negativity. *B*: evidence for synchronous oscillation of neuronal discharge across the motor cortex. CCGs for 3 pairs of wires compiled from the data shown in Fig. 4 (Gaussian SD: 2 ms). Height of central peak indicates synchronous activation, prominence of sidebands correlates with synchronous oscillation of cells at the 2 sites. Synchrony may occur over large distances, as for sites 21 and 7 that were separated by >5 mm.

Synchrony of motor cortical LFP oscillations and MU activity

Correlation methods were used to determine the temporal relationships among neural discharge and LFP signals. Cross-correlograms (CCGs) compiled for the two signals recorded during the finger force task (Fig. 8*A*) demonstrated that MU firing tended to occur near the LFP peak negativity at both *overlapping* (wires 7, 13, and 21) and *mixed* (wires 18 and 20) sites. This is consistent with the hypothesis that MU firing at a site may be coupled to processes producing LFP oscillations at that location. To evaluate the apparent temporal coherence of MU or LFP signals between cortical locations, we computed CCGs from pairs of simultaneously recorded sites. Previously we demonstrated broad coherence of the LFP across motor cortex during motor preparation as well as the diminished coherence during finger force and wrist extension actions in both of these same monkeys (Sanes and Donoghue 1993). Results using LFP records of different finger force trials agree fully with those earlier findings and are therefore not shown here. Cross-correlation analysis of neural discharge revealed coherence in this signal across motor cortex. CCGs from three of four pairings of neurons showing the most pronounced oscillations in *monkey FC* contained central peaks ~0 ms, indicative of synchronous activation, in addition to side-band peaks at about ±20–30 ms, features consistent with fast co-oscillation of the two signals (Fig. 8*B*). Synchronous and oscillatory MU activity occurred not only between nearby sites but also in one case between two sites (wires 18 and 21) separated by ~5 mm. The remaining cell pair examined in *FC* and each of five pairs examined in *FD* showed central peaks but lacked sidebands, indicating the occurrence of synchrony in the absence of overt oscillations. Inspection of recordings revealed that periodic MU discharge did not occur concurrently across all cortical sites and that oscillatory episodes lasted only briefly, in the range of a few hundred ms (e.g., Fig. 5, time period for wires 18 and 20, ↑).

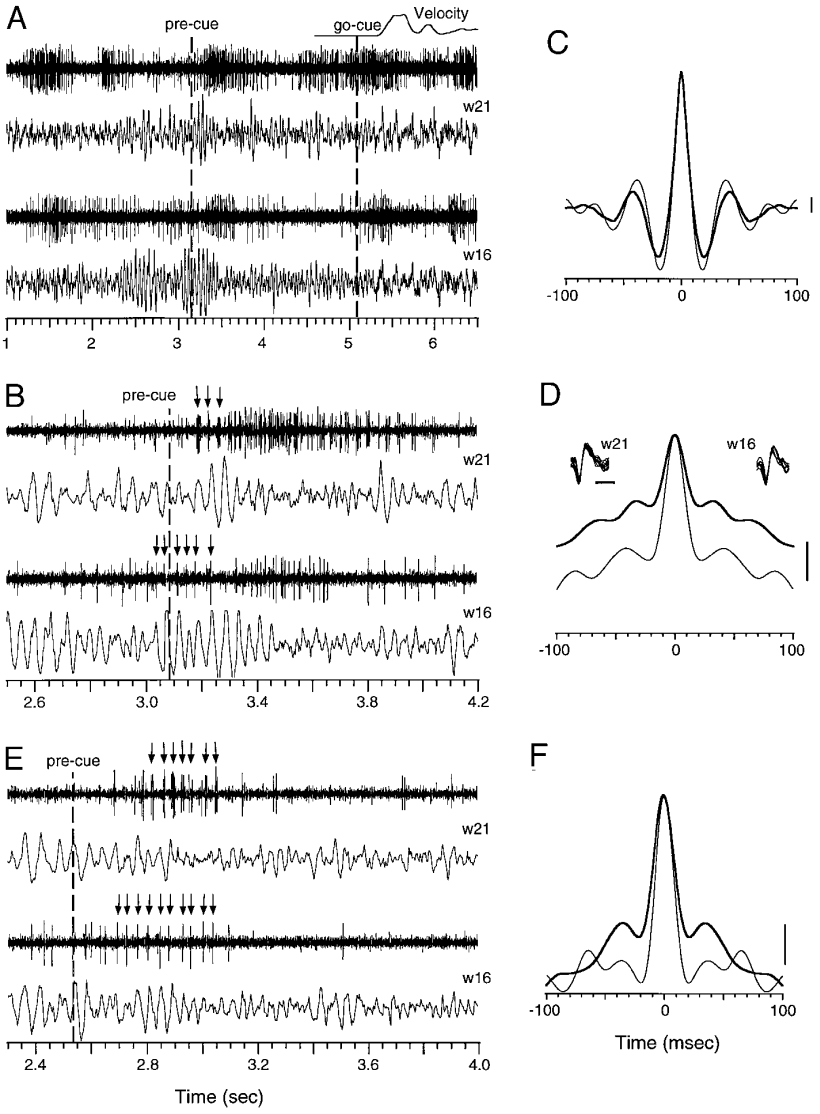

FIG. 9. Neural discharge and LFP activity during the three direction reaching task for *monkey FD*. *A*: simultaneous recordings from wires 21 and 16 during hold, preparatory, and action periods. Direction of movement was instructed at the precue (1st dashed line) with the go-cue delivered at second dashed line. Movement onset is indicated by first upward deflection in the tangential velocity trace (*above topmost MU record* in *A*). LFP filtered records for each site appear below corresponding unit traces. At these sites, discharge increased around the time of the cue and with movement execution. Similar to finger actions, LFP oscillations were evident in the period before movement, but not during movement. *B*: time expansion from data in *A*. Note the regular interspike intervals associated with prominent LFP oscillations. *C*: ACGs from LFP record for wire 21 (thick line) and wire 16 (thin line). *D*: ACGs compiled from this single trial for individual neurons discriminated from record shown in *A* (format as in *C*). Examples of the spike waveforms used for ACGs are shown (*top right* and *left*). Side peaks in the correlogram are consistent with fast oscillatory discharge of these cells. *E*: periodic appearance of discharge in preparatory period for the same sites (wires 21 and 16) during a different trial. *F*: ACG for the units recorded in trial shown in *E*.

Oscillations during conditioned reaching movements

After neural recording in the finger force task, *monkey FD* was trained to perform the three direction reaching task. This task was used to examine LFP and neural discharge during planar arm movements requiring transport of the hand to a target, in contrast to the more motorically constrained isometric finger actions. In the reaching task, the direction of the upcoming movement was unspecified until precue appearance, which separated the hold and preparatory periods. Therefore, preparation for direction could occur only after the precue.

Six sites with MU activity modulation associated with the finger force task also showed modulation during the reaching task (Fig. 1*B*, ⊕). These six sites also exhibited LFP oscillations during reaching similar to that seen during the finger force task. Figure 9 illustrates examples of recordings obtained simultaneously from two sites that contained discriminable units (wires 21 and 16, see *insets* in Fig. 9*D*). It could not be determined with certainty whether the same neurons were recorded during both tasks, although for wire 21, a single large unit of similar wave shape was prominent throughout the course of these experiments. Well-isolated neurons were not evident at the other sites. As in the digit task, LFP oscillations occurred before but diminished during reaching at all sites, even though the motoric features of reaching and the accompanying neural discharge pattern differed substantially from those of the finger force task. For example, neural activity recorded from wire 21 in *FD* decreased during motor action in the finger force task (Fig. 2*B*) but increased during reaching (Fig. 9*A*). However, for both tasks, LFP oscillations at this site occurred before motor action onset and were infrequent during the motor action (compare reaching data in Fig. 9*A* with finger force data in Fig. 1 of Sanes and Donoghue 1993). For reaches in all directions, LFP oscillations occurred before (hold period) and after (preparation period) direction of the upcoming movement was instructed, thereby indicating that LFP oscillations do not specify the direction of upcoming action. Further, no readily apparent differences in the pattern, form, or timing of oscillations were observed in trials requiring different movement directions even though the neural discharge showed directional tuning. Several other features of oscillations and discharge remained constant across the two

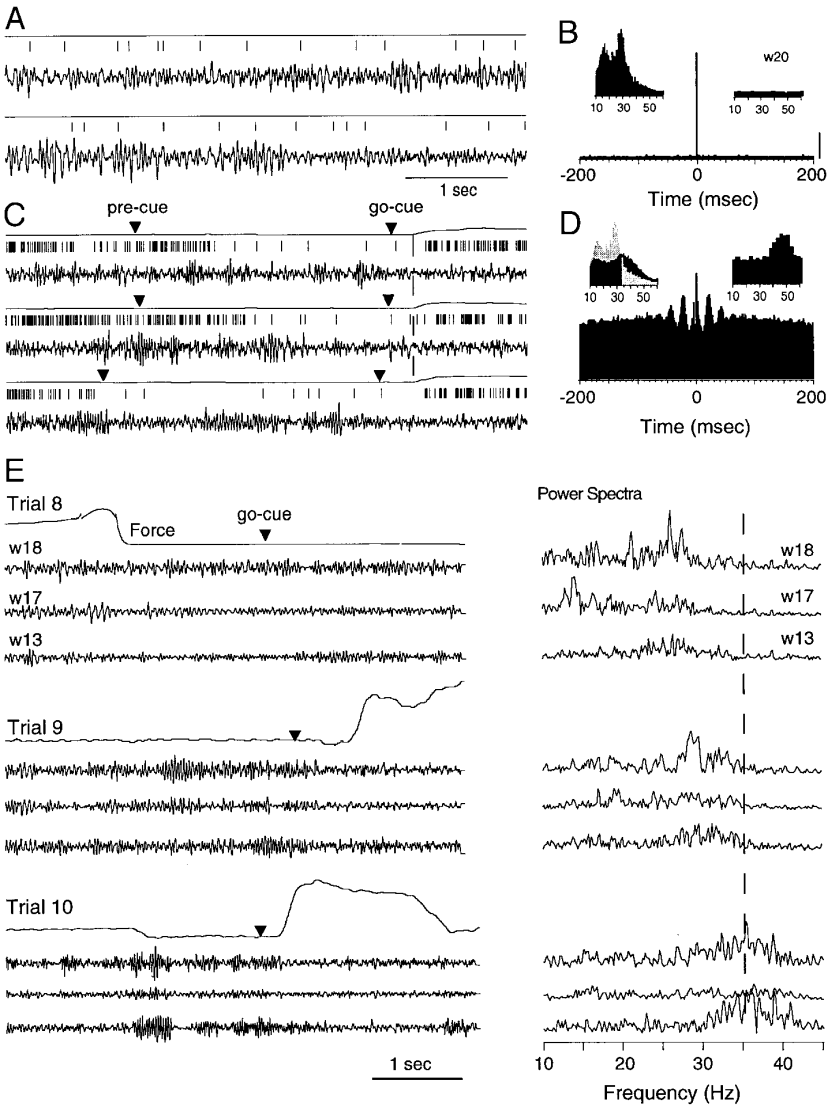

FIG. 10. Appearance of fast oscillations associated with task engagement. *A*: force records (*top row*), discriminated MU activity (vertical hatch marks, *middle row*) and LFP recordings (*bottom row*) for 2 separate periods when the monkey was sitting quietly in the dark with the video monitor off. *B*: ACG of MU activity calculated during approximately 1 min of quiet sitting (*center*). *Left inset*: spectrogram from LFP data; *right inset*: spectrogram from MU data during this period. Spectrograms are not normalized. *C*: data from three finger force trials after the inactive period depicted in *A.* First arrowhead in the trial marks the precue and the second arrowhead marks the go-cue. Note that LFP frequency increases during task engagement in comparison to that obtained during quiet sitting. Task-related modulation of MU activity also begins in association with onset of finger force. *D*: ACGs and spectrograms for recordings obtained from the same site during performance of the finger force task. LFP power spectrum during inactivity (copied from *C,* gray shading) is superimposed on spectrum during task performance (black). Note that the LFP power decreases in the lower frequencies and shifts to the 35- to 50-Hz range with task engagement. Also note the strong oscillatory nature of the MU discharge at this site during. *E*: shift to higher frequencies with commencement of task performance. Here 3 successive trials are shown with the last (*trial 10*) being the 1st correctly performed (i.e., reinforced) finger action after a period of inactivity. Force records show finger action around time of request to move. *Right*: LFP power spectra for the trials on the *left.* Note the shift to higher frequencies over successive trials, so that higher frequencies are only evident when the conditioned task is being performed. Nevertheless, these higher frequency components cease with motor action.

tasks for all sites evaluated. Classification of the relationship between LFP oscillations and discharge yielded three mixed and three overlapping patterns, matching that observed in the finger force task. Periodic MU discharge was also evident during the reaching task (arrows, Fig. 9, *B, C,* and *E*). ACGs compiled from individual trials of single unit discharge contained side bands in the 24–36 Hz range (Fig. 9, *D* and *F*) suggestive of oscillatory firing. It was, however, possible to find apparently periodic discharge without prominent LFP oscillations at the same time (Fig. 9*E,* wire 21, arrows) indicating that regular bursts of discharge can occur in the absence of LFP oscillations.

Relationship of oscillations to task engagement

The prevalence of LFP and neural discharge oscillations during holding and preparation and their cessation during motor actions in operantly conditioned arm and finger tasks could signify a relationship to the general motor inactivity occurring at these times. Consequently, we tested whether fast oscillations occurred during periods of quiet sitting interposed between active task performance. Figure 10 illustrates the differences between the recordings obtained from wire 20 in these two conditions for *monkey FC.* While the monkey sat quietly, MU discharge rate was low and unstructured (Fig. 10*A* and ACG in Fig. 10*B*). The power spectrum of the MU ACG compiled during quiet sitting was flat between 10 and 60 Hz (Fig. 10*B, right inset*). By contrast, when the monkey subsequently commenced task performance, MU activity showed task-related modulation (see also histograms in Fig. 2) and periodic discharge (Fig. 10*D,* also Fig. 7). Concomitantly, LFP oscillations in the 35- to 50-Hz range became more pronounced with a drop-off in power at lower frequencies (Fig. 10*D*). On resuming the task, a shift to high-frequency LFP oscillations and increased background MU activity became evident with the first actions. This effect is demonstrated in LFP and force records and concomitant power spectra from three trials illustrating the transition from no task performance (Fig. 10*E, trial 8*) to the first ''correctly'' performed trial (Fig. 10*E, trial 10*). The power spectra show the shift in the LFP toward higher frequencies. These results suggest that fast oscillations signal a general form of task engagement. Similar results were obtained at the other sites recorded in *FC.* In *monkey FD,* only LFP

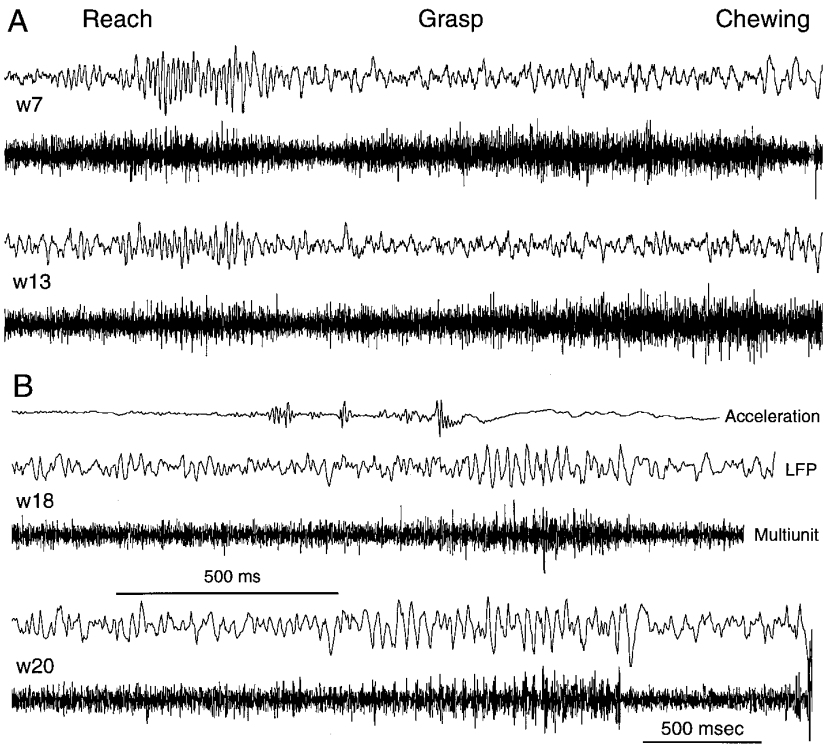

FIG. 11. Neural activity and LFPs during spontaneous reach and grasp movements. *A*: LFP and MU filtered records from 2 simultaneously recorded sites. Note increased MU activity at early and late phases of the movement but the occurrence of LFP oscillations only in the initial phase. Approximate time of reach and grasp action is indicated. *B*: example of LFP oscillations that infrequently accompanied increased neural discharge during terminal phases of reach and grasp movement. Hand acceleration appears at the *top*, indicating hand actions.

signals were recorded once during the sitting and task performance conditions. In this monkey, the shift to higher frequency was less marked because power spectra were multipeaked and fast oscillations were of generally lower frequency, so they blended more into the broadband form of the power spectrum. Nevertheless, increased power in the 24- to 40-Hz range emerged with task engagement in this monkey as well.

Oscillations during exploratory movements

Upon production of a trained finger or arm reaching actions, we observed a cessation of oscillations among a set of sites believed to be closely related to motor action because of their task-related neuronal discharge modulation. Both tasks used were operantly conditioned and overtrained. The observations of Murthy and Fetz (1992) suggested that fast oscillations might occur at such sites during movement if the movements were untrained or exploratory. Consequently, we recorded MU and LFP activity when *FC* reached into a bowl and retrieved a food morsel without direct sight of the pellet. We termed the first half of the trial, reach, and the later half, grasp, although the instrumentation used did not allow us to distinguish precisely when either period began or ended. Five sites that exhibited task modulation during the finger force task (see Fig. 1) also showed firing rate modulation (Fig. 11) either during the reach, the grasp, or both. LFP oscillations occurred during these trials, most commonly early in the trial and less frequently during the grasp. Figure 11*A* illustrates the most frequently encountered case in which grasp was marked by elevated neural discharge without fast oscillations in the concurrent LFP recording from that site. By contrast, Fig. 11*B* illustrates a more atypical case in which LFP oscillations overlapped periodic MU discharge during the grasp. For each of the wires, LFP oscillations occurred at the beginning of the reach phase in nearly all trials ($>$80% of 50 successive trials examined for the set of 5 wires). Across the set of sites oscillations occurred for $\sim$10% of trials during the grasp phase, except for one site in which reach-period oscillations were present in 40% of the trials during the terminal phases of movement. For the same data set, periodic MU discharge could be observed in $\leq$50% of the trials during the reach and in 10–20% of the trials during the grasp, depending on which wire was examined. These data indicate that LFP or MU oscillations occur, but only irregularly, in association with untrained reaching movements.

DISCUSSION

These studies demonstrate the widespread occurrence of fast oscillations in LFPs and in neural discharge within monkey motor cortex during trained and unpracticed motor actions. Fast LFP oscillations occur at sites where nearby, simultaneously recorded neurons show task-related neural discharge modulation around movement onset, but oscillations do not reliably reveal underlying firing patterns related to movement. Instead, diverse and complex relationships exist between fast LFP oscillations and neural discharge. The timing of oscillatory episodes with respect to the production of movement varies so that oscillations are rare during operantly trained motor actions, but occur irregularly during untrained reach and grasp movements. During delays in advance of movement, oscillations are prominent. At some sites, they are concurrent with discharge that occurs over this period, however, at other, simultaneously recorded sites, neural discharge mainly is negatively correlated with the appearance of oscillatory episodes. Despite the complex

linkage to neural discharge, oscillations appear to be related to active behavior because they emerge as soon as the monkey engages in a motor task. These observations suggest that oscillations establish spatiotemporal activity patterns separable from those found in neural discharge. Oscillations must represent processes ongoing in neocortex not related to specific aspects of movement that are encoded by neural discharge within that region but rather to more abstract or global features of active behaviors. Both neural discharge and oscillations develop patterns of synchronous activation across motor cortex, suggesting that temporal codes, in addition to firing rate codes, may operate among populations of motor cortex neurons as they become engaged in the production of various motor behaviors.

Coupling of LFP oscillations to neural discharge

To discuss the relationship of neural discharge to oscillations in the trained tasks, it is useful to consider three periods: *1*) the premovement delay, in which the monkey gets instructions and awaits a go cue; *2*) the period immediately around movement onset, when motor action begins; and *3*) the period of steady holding after the target is reached. Working backward, the clearest and most consistent relationship is the relative scarcity of oscillations after movement begins (*3*). This is common to all sites we have recorded in a variety of trained finger, wrist, and arm-reaching tasks (see also Sanes and Donoghue 1993). We know that this pattern occurs across MI whether or not movement-related discharge increases are evident at that site. The period around movement onset (*2*) was the most complex because oscillations were present at some sites and not at others and they varied from trial to trial, even at sites where neural discharge was consistently elevated at this time (as in Fig. 3, W7). During the premovement delay (*1*), oscillations and neural discharge also exhibited complex relationships, but with more consistency than in 2. During this time of holding and preparation awaiting a cue to move, we defined overlapping and mixed patterns. For a particular task, these patterns were relatively consistent at a site, suggesting that the two signals are mechanistically linked. The overlapping sites (38%) were the only ones where it appeared that oscillations were predictive of elevated neural discharge. This pattern fits best with data from visual cortex that suggest a close link between stimulus-driven discharge and LFP oscillations at the same site (Eckhorn et al. 1988, 1993; Gray and Singer 1989; Gray et al. 1989; Kreiter and Singer 1992). At mixed sites, discharge was largely the complement of delay period firing but some overlap was also evident. Particularly intriguing were periods during which apparently aperiodic activity became briefly periodic and then ceased. Here, LFP oscillations commenced during the periodic phase of discharge but then continued during a time when discharge diminished (see Fig. 4). Although the significance of this pattern is unclear, it suggests that an interplay between the source of LFP oscillations and neural discharge can establish complex patterns across cortex. Because we used simultaneous multichannel recordings, we know that these various patterns of LFP and neural discharge occur simultaneously across cortex during individual movements.

Diversity in the relationship between LFP oscillations and neural discharge is not peculiar to our data. Reciprocity of the two signals is evident in recordings from cat visual cortex (Eckhorn and Obermueller 1993; Ghose and Freeman 1992; Gray et al. 1992) as well as in other recordings from *monkey MI* (Murthy and Fetz 1992). In visual cortex, oscillatory LFP responses occur without detectable spike activity when stimuli are presented to orientation-tuned cells in their nonpreferred direction or when more global stimuli are used (Bauer et al. 1995; Eckhorn and Obermueller 1993; Gray et al. 1992). In motor cortex, the nature of inputs is more complex and may be considerably different from well-controlled stimuli used to drive visual neurons. Our results are generally incompatible with the view that fast LFP oscillations predict neural spiking at a site.

As reported by Murthy and Fetz (1996) and confirmed by our data, LFP oscillations accompanied neural discharge associated with prehensile movements that were not explicitly trained. Our experiments show that this pattern occurs at the same sites where LFP oscillations cease with trained motor actions. However, in the untrained prehensile tasks, the relationship of LFP oscillations to neural discharge was nevertheless temporally inconsistent. Thus the idea that oscillations reflect neural discharge during prehensile or untrained movements also must be rejected.

In our data, ACGs mainly from MU, but also from single-unit recordings, indicated periodic discharge (Figs. 7–10) at 63% of the recorded sites, suggesting that a subset of neurons in motor cortex are fast oscillators. In agreement with our findings, around one-half of all neurons sampled in motor (Murthy and Fetz 1996b) and visual (Gray and Singer 1989; Gray et al. 1989; Livingstone 1996) cortex also show these properties. Although many have reported oscillating neurons in cortex (Ghose and Freeman 1992; Gray et al. 1990; Livingstone 1996; Murthy and Fetz 1992, 1996a,b), others have found very few (Nakamura et al. 1992; Tovee and Rolls 1992; Young et al. 1992; but see Singer 1993). Because cortical neurons can participate irregularly in periodic bursts field oscillations (Buzsakí et al. 1992; Eckhorn and Obermueller 1993), the summing of many cells with MU recordings may improve the probability of detecting oscillatory neurons. We also noted that discharge oscillations were more difficult to observe in single cell recordings. Periodic patterns in autocorrelations may be diluted when the brief oscillatory episodes of single cells are mixed with aperiodic spiking (Murthy and Fetz 1996b).

Origin of fast oscillations in motor cortex

The dissociation of LFP oscillations and neural discharge during delay or motor action phases or in association with different types of tasks seems enigmatic. However, current flow related to slower, synaptic potentials predominate in field potential recordings while there is less contribution of the rapid current flux related to action potentials (Mitzdorf and Singer 1978). Thus a likely origin of fast LFP oscillations is locally correlated membrane potential fluctuations for groups of cells that may be driven by input from other sources. In some instances, these oscillations may produce suprathreshold activation, which would account for the correspondence of LFP and MU discharge and oscillatory spiking (Fig. 8). The strong phase locking of spiking during

LFP oscillations (Murthy and Fetz 1996b) supports a local origin of the LFP oscillation. At other times, LFP oscillations must be subthreshold because there is no associated spiking of cells at the recording site. Subthreshold oscillations have been demonstrated in intracellular recordings from MI neurons (Murthy et al. 1994), but the interrelationships of discharge and oscillations in trained delay tasks was not investigated in that study. Differences in the form of LFP oscillations across cortex, as we observed during simultaneous recordings, suggest that LFP oscillations establish a complex pattern across cortex during which time the membrane potentials of a large number of MI neurons are adjusted but not necessarily brought to a point of interaction through spiking. What holds cells in an oscillatory, but subthreshold mode during specific behavioral epochs, such as movement preparation, would be of interest to explore. Nonperiodic spiking in the fast range, which is seen commonly in our records during both trained and untrained motor actions, necessarily would be generated by inputs that are either aperiodic themselves or do not engage oscillatory mechanisms. The rarity of fast oscillations during intense movement-related discharge (e.g., Fig. 7*C*) rules out the possibility that oscillations simply emerge as a consequence of intense discharge.

Fast LFP oscillations in the absence of local firing would appear to require other origins, unless a set of oscillatory cells are consistently missed in our recordings. One potential origin is volume conduction of oscillatory signals from distant sites, but the observation that LFP oscillations can begin in synchrony with local neural discharge oscillation and then continue (e.g., Fig. 4, wire 20) seems more parsimoniously explained by a local mechanism. Fast LFP oscillations also could be generated by inputs that are oscillatory themselves; these could originate from extrinsic sources or from within motor cortex. Local differences in timing, amplitude, and form observed in fast oscillations recorded simultaneously in cortex suggest that there is considerable independence among their generators and that fast oscillations do not merely reflect a common global input that is itself oscillatory (see discussion in Singer and Gray 1995; Steriade et al. 1996) (see examples in Figs. 3 and 4, wires 13 and 18, just before and after the precue). Differences in the structure of MU CCGs (Fig. 8*B*) between sites in motor cortex is also consistent with this view.

Relationship of oscillations to motor behavior

Fast oscillations in the LFP and in neuronal discharge emerge across motor cortex with the transition from quiet sitting to task engagement, and they appear in association with a variety of motor actions (Fig. 10). Therefore fast oscillations appear to be related to an active process that ordinarily is coupled to voluntary motor action. However, their variability with respect to behavior, and often to the ongoing neural discharge at the same cortical site, suggests that fast oscillations themselves reflect a more global process rather than specific details of the upcoming motor action.

At least two types of temporal variability were present. First, oscillations recorded at the same set of cortical sites shifted from the premovement period to overlap with movement performance when untrained reaching movements were performed. Murthy and Fetz (1996a) also found oscillations in MI during a similar free reaching task, and they found that oscillations were infrequent in repetitive ramp and hold wrist movements, but no comparisons were made for the same sites in different tasks. Why oscillations occur often but sporadically during exploratory movements and much less frequently during the realization of trained movements is unclear. Clues may emerge from differences in the nature of the tasks. One important difference in these tasks is that detailed planning is possible during premovement hold periods in the conditioned tasks we used, whereas planning is presumably ongoing during the free reaching tasks. Thus fast oscillations during untrained actions may reflect the same global processes that are completed when there is time to prepare movement but overlap movement when preparation, attentive-related processes, and movement must be simultaneously processed. The finding that oscillations emerge across MI when task engagement begins, even during periods lacking overt performance of the task, is consistent with this view. We also noted that a significant increase in the power spectrum at some sites after the precue, suggesting that the appearance of the oscillations may be linked to motor preparation that began in this period. However, oscillations were evident both in the hold (when no details about upcoming movement were available) and preparatory periods (when the target was specified) so that they could not be specifically related to details of the upcoming movement unless a default motor strategy was planned in advance of the instruction cue. Which of these processes, if any, produce oscillations cannot be determined presently: attention, motivation, readiness, or some planning process seem to be viable alternatives at the present time.

A second form of variability was the irregular occurrence of oscillations with respect to behavioral events within a trial. This trial-to-trial variability in the relationship of oscillations to movement onset or the appearance of a visual cue suggests that fast oscillations cannot be coupled too tightly to any particular detail of the task. In this regard, Murthy and Fetz (1996a) found that LFP oscillations are not time locked to EMG onset. The looseness of the correlation between oscillations and external events is not peculiar to motor cortex. Variability in the onset times of both LFP and unit oscillations to sensory stimuli have been noted in visual cortex as well (Eckhorn 1994; Livingstone 1996).

The present study extends observations about the cessation of fast LFP oscillations with finger or wrist movements to include conditioned arm reaching movements. There were no striking differences in oscillation patterns when we varied movement or isometric conditions or body parts used (finger vs. whole arm). Fast oscillations occurred during visually guided actions and when grasping movements were made out of view. Therefore it is unlikely that oscillations at a single site have much of a specific relationship to the selection of limb segments, implementation of single or multijoint movements, or with distinctions in visually or nonvisually guided actions.

Together, these findings indicate that fast oscillations are related to a specific cortical state. A connection between fast oscillations and attentive or vigilance states has been suggested previously (Bouyer et al. 1981; Montaron et al. 1982; Ribary et al. 1991; Sheer 1984, 1989). LFP oscillations have been reported in association with ''attentive''

behavior in the visual cortex of cats (Bekisz and Wróbel 1993) and dogs (Lopes da Silva et al. 1970) and in somatic sensorimotor cortex of cats and monkeys (Bouyer et al. 1987; Rougeul et al. 1979). We would extend these observations to include fast neural discharge oscillations as well. Magnetoencephalographic studies in humans found 40 Hz activity associated with wakefulness and rapid eye movement but not slow wave sleep, which is also supportive of a relationship of fast oscillations with active brain states (Llinás and Ribary 1993). These findings suggest that oscillations in visual cortex would be influenced by attentive demands.

Based on recordings in rat and rabbit olfactory cortex, Freeman (Freeman 1978; Freeman and Skarda 1985) suggested that the spatiotemporal coordination of neuronal groups emerges by their synchronous oscillation (see INTRODUCTION). During movement, spatial and temporal coordination are critical parameters (Bizzi et al. 1991; Flanders 1991; Shadmehr and Arbib 1992) that may employ oscillations for their implementation. Thus oscillations may be a means to facilitate widespread synaptic coupling or binding of selected groups of neurons but not to specify details of their ongoing operations or even necessarily produce firing. Recently it has been proposed that oscillations may specifically help in establishing long-range synchrony among cortical neurons (Rolfsema et al. 1996). Because they appear to be linked to preparatory functions, oscillations could reflect attempts to couple MI with cortical areas related to movement preparation. One candidate are the premotor areas; premotor cells with delay activity can turn off at movement onset (Weinrich and Wise 1982), just as oscillations do. Whether cells with preparatory activity in premotor cortex provide this signal remains to be determined.

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