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Changes in power and coherence of brain activity in human sensorimotor cortex during performance of visuomotor tasks

F. Aoki [a,*], E.E. Fetz [a], L. Shupe [a], E. Lettich [b], G.A. Ojemann [b]

[a] *Department of Physiology and Biophysics, University of Washington, Seattle, WA 98195-7290, USA*
[b] *Department of Neurological Surgery, University of Washington, Seattle, WA 98195, USA*

Abstract

Electrocorticograms (ECoG) were recorded using subdural grid electrodes in forearm sensorimotor cortex of six human subjects. The subjects performed three visuomotor tasks, tracking a moving visual target with a joystick-controlled cursor; threading pieces of tubing; and pinching the fingers sequentially against the thumb. Control conditions were resting and active wrist extension. ECoGs were recorded at 14 sites in hand- and arm-sensorimotor area, functionally identified with electrical stimulation. For each behavior we computed spectral power of ECoG in each site and coherence in all pair-wise sites. In three out of six subjects, γ-oscillations were observed when the subjects started the tasks. All subjects showed widespread power decrease in the range of 11–20 Hz and power increase in the 31–60 Hz ranges during performance of the visuomotor tasks. The changes in γ-range power were more vigorous during the tracking and threading tasks compared with the wrist extension. Coherence analysis also showed similar task-related changes in coherence estimates. In contrast to the power changes, coherence estimates increased not only in γ-range but also at lower frequencies during the manipulative visuomotor tasks. Paired sites with significant increases in coherence estimates were located within and between sensory and motor areas. These results support the hypothesis that coherent cortical activity may play a role in sensorimotor integration or attention. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Brain activity; Human sensorimotor cortex; Electrocorticograms

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1. Introduction

Oscillatory brain activity in the γ-frequency range (30–80 Hz) has been observed in various cortical areas of mammalian brain in relation to olfactory perception (Bressler and Freeman, 1980; Freeman, 1991; Freeman and Skarda, 1985; Laurent et al., 1996), visual perception (Freeman and van Dijk, 1987; Eckhorn et al., 1988; Gray et al., 1989) and perceptual motor tasks (Murthy and Fetz, 1992; Sanes and Donoghue, 1993). The possible function of such γ-activity has been debated vigorously (Gray, 1994; Pantev et al., 1994; Singer, 1994; MacKay, 1997). In visual system, synchronous oscillations have been postulated to link neuronal assemblies representing different features that are integrated into a unified percept

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[*] Corresponding author. Present address: Karolinska Institutet, Department of Medical Science & Technology, Division of Clinical Neurophysiology, Huddinge University Hospital, S-141 86, Sweden.

E-mail address: fumi.aoki@neuro.ki.se (F. Aoki).

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and to separate figure from ground (Singer, 1993, 1994; Singer and Gray, 1995; Roelfsema et al., 1997). Thus, synchronization of activities in distributed neuronal populations could play an important role for the binding function. A comparable role for synchronized oscillations in motor process has been also debated (Murthy et al., 1994; Roelfsema et al., 1996; MacKay, 1997). The oscillatory activities in sensorimotor cortex would facilitate associations between neuronal populations involved in the same task (Murthy and Fetz, 1992, 1996b).

In human brain, inter-regional coherent activity has been studied mainly using conventional electroencephalography. Coherent activity was found in multiple regions during perceptual motor task (Tremblay et al., 1994; Classen et al., 1998; Rodriguez et al., 1999) and in relation to associative learning (Miltner et al., 1999). Compared with conventional EEG recording, electrocorticography (ECoG) using a grid of subdural electrodes provides high sensitivity and high spatial resolution. A previous study using the ECoG of subjects performing a somatosensory discrimination task showed no evidence for globally correlated activity in the γ-frequency range (Menon et al., 1996). The present study using ECoG shows increase in γ-range activity in the sensorimotor cortex of human subjects performing manipulative visuomotor tasks and provides an evidence for synchronization of γ-activity using cycle-triggered averages and cross-spectra. A preliminary result of coherence analysis in all pair-wise sites shows that coherence estimates increase within and between sensory and motor sites during task performance. Detailed results from spectral analysis were documented in another report (Aoki et al., 1999).

2. Methods

Subjects were six patients with intractable epilepsy who were planned to undergo surgical treatment. The subjects gave written informed consent to participate in the study. One week before cortical resections, a subdural electrode grid composed of 64 stainless steel electrodes separated by inter-electrode distances of 1 cm, was implanted over the fronto-parietal-temporal region contralateral to the side of seizures. The subjects were monitored continuously for 7 days to localize the seizure focus. Before the recording sessions, we obtained functional maps of the cortical sites by delivering electrical stimuli through the implanted subdural electrodes. Functionally identified sites are indicated on the illustrated electrode grids by letters indicating motor (M) or sensory (S) responses evoked at different somatic loci in hand (h), arm (a), face (f), trunk (t) or leg (l).

The subjects, seated comfortably in bed with the back supported, performed three visuomotor tasks, target tracking, threading and finger sequencing. In the tracking task, the subjects followed a moving target on a monitor with a cursor that was controlled by a joystick. In the threading task, the subjects threaded pieces of tubings. In the finger sequencing, the subjects made sequential pinches between the thumb and other fingers from index to little finger and then in reverse order. Control activity was recorded before the task sessions when the subjects were resting with their eyes open; then the subjects performed a wrist extension for 2–20 s as movement control.

ECoGs were recorded from 14 sites, including the sites in forearm sensorimotor cortex identified by functional mapping and some adjacent sites. Electromyograms (EMG) from extensor carpi and thumb adductor of the active hand were recorded with surface electrodes in all conditions. During the tracking task, the movement of the joystick, measured as the x and y coordinates of the cursor, was recorded simultaneously with the ECoG and EMG. Movement onset for the task performance was estimated on the basis of EMG activity and joystick movement. The ECoG was band-pass-filtered from 0.5 to 120 Hz (3 dB point; -12 dB per oct) and the EMG from 5 to 500 Hz. The data were stored on cassette tapes in analog form for off-line analysis.

2.1. Data analysis

The ECoG signals were displayed on an oscilloscope together with the EMG and the joystick movement, and were inspected for appearance of γ-range oscillation during the task performance.

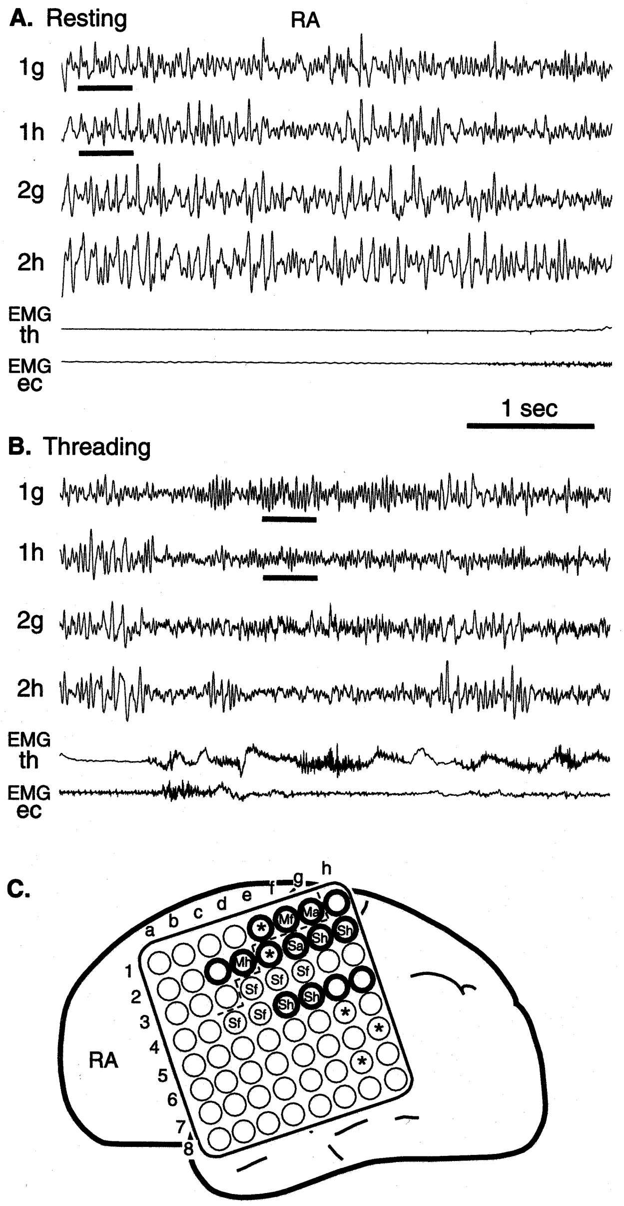

Fig. 1. Cortical activity of subject RA. Traces show ECoG from sites 1g, 1h, 2g and 2h and EMG of thumb adductor and extensor carpi radialis. (A) During rest. ECoGs showed 10–30 Hz oscillations. (B) During threading. Sites 1g and 1h exhibited intermittent 30–40 Hz oscillations. (C) Schematic of electrode grid. Thick circles indicate the analyzed recording sites. Functional mapping by direct electrical stimulation identified some sites as motor (M) or sensory (S); lowercase letters indicate somatic location, hand (h), arm (a), face (f). Sites with an asterisk (*) were identified in long-term recordings as sites where epileptic activity first appeared at onset of seizures.

For power spectrum and coherence analysis, all the ECoG signals were digitized and stored with a 12-bit resolution at a sampling rate of 512 Hz. The fast Fourier transform (FFT) was computed for successive 1 s windows (512 points) using Hanning window taken sequentially with a 0.5 s shift during the period for each task condition. Each power spectrum was divided into five frequency bands, 11–20; 21–30; 31–40; 41–50; and 51–60 Hz. Significance of the power changes in each frequency band between the resting and each task condition was measured by the Mann–Whitney *U*-test. Coherence estimates were calculated by averaging normalized complex cross-spectral density within bands and time-epochs (Saltzberg et al., 1986). The coherence value was analyzed for all pair-wise combinations of electrode sites for successive 250-ms window, divided into seven to eight frequency bands, (1–10); 11–20; 21–30; 31–40; 41–50; 51–60; 61–70; and 71–80 Hz, and averaged over every 2-s data section (eight epochs). Significant changes in coherence estimates between the resting and each task condition were estimated by the Mann–Whitney *U*-test using averaged coherence values.

3. Results

3.1. γ-Oscillation in relation to task performance

In three subjects, overt γ-oscillations appeared during the visual motor tasks. Fig. 1 shows ECoG activities from subject RA. In this subject, α-range oscillations were dominant during the resting period (Fig. 1A). γ-Oscillations appeared in four sites, an arm motor site 1g and sensory sites 1h, 2g, and 2h when the subject started the threading task (Fig. 1B and C). Power density distribution at the underlined parts in 1g and 1h shows a peak around 10 Hz during the resting, and a peak at 35–40 Hz during the threading (Fig. 2). Fig. 3 shows the time series of the power in α- and γ-bands for the two sites. When the subject started the task, the power of 9–12 Hz decreased and that of 35–38 Hz increased in both 1g and 1h. We performed power density analysis in all subjects for all task conditions and compared between the task and resting conditions. In all subjects, α–β (11–20 Hz) range power decreased and γ-range power increased at sensorimotor sites during task performances.

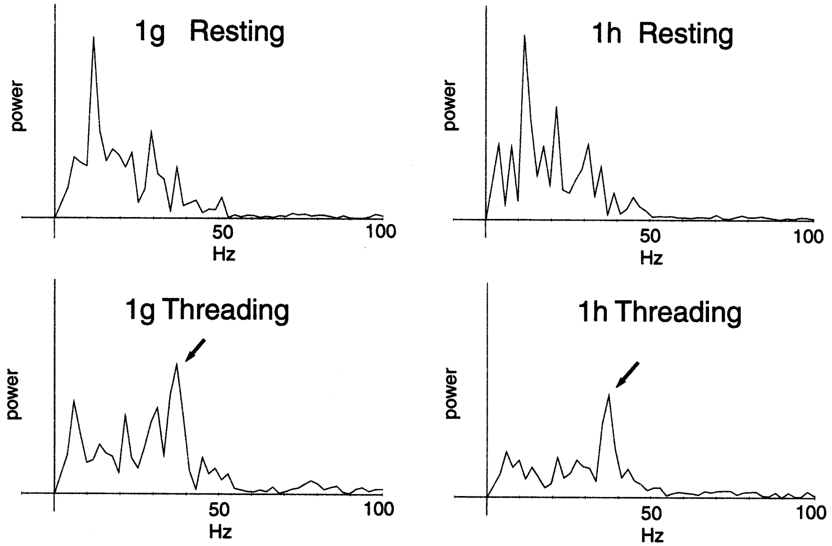

Fig. 2. Power spectra of the signals in sites 1g and 1h underlined in Fig. 1A and B.

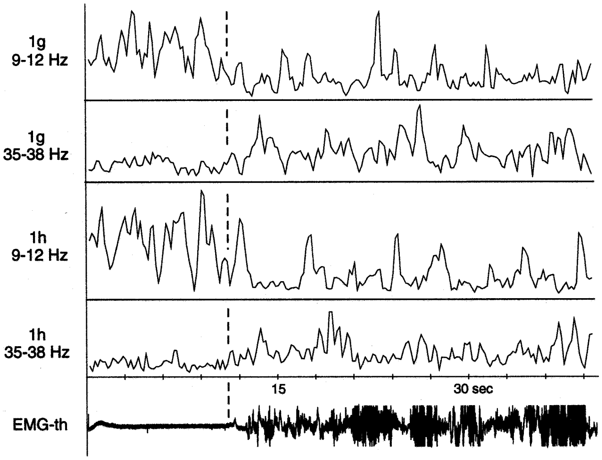

Fig. 3. Running record of the power in low- and high-frequency bands for 1g and 1h of subject RA, before and after onset of the threading task, as indicated by the EMG of thumb adductor (bottom).

3.2. Task related change in power

Spatial distribution of the sites, where γ-range power significantly increased, depends on the sensorimotor tasks. Fig. 4 shows spatial pattern of power changes in different task conditions for subject RA. During the threading task, the power in 31–60 Hz increased vigorously in sensorimotor sites. In contrast, during the wrist extension task, changes in the power, especially in the γ-range, were trivial. The spatial pattern of increases in γ-range power during the threading is similar to that during the finger sequencing task—that is, γ-range power increased significantly in 1g, 1h, 2e–h. In contrast, during the tracking task, γ-range power increased significantly only in 1g, 2e, and 2h, suggesting the spatial pattern of power changes is specific to the tasks. In all subjects who performed all four tasks, γ-range power increased more significantly and in more sites during the visual motor tasks compared with during the wrist extension task.

3.3. Synchronization of γ-oscillation

The increase in γ-range power during the visual motor tasks is evident by spectral analysis. To show synchronization of γ-range activity, we computed cycle-triggered averages (CTA) and cross-spectra. Fig. 5 shows ECoG activities during the resting (Fig. 5A) and target tracking (Fig. 5B) in another subject CK. In this subject, interictal activities appeared synchronously in many sites. When the subject started the task, these activities decreased and γ-oscillations appeared in 5g (a motor site) and 7e (a sensory site; Fig. 5C). In CTA, ECoG activity in each site was averaged using each cycle of γ-oscillations in 5g as trigger (Fig. 6). The CTA showed that the largest amount of synchronization occurred with negligible phase lag between 5g and 7e. Cross-spectra between the two sites were computed as FFT of cross-correlation function between two signals with 512 ms windows during every 5 s. The cross-spectra between the spatially separated sites 5g and 7e showed a peak in 35–50 Hz during the target tracking, but not during either rest, wrist extension, or finger sequencing (Fig. 7). These data indicate that synchronization of γ-oscillations between the two sites occurs dependent on behavioral condition.

3.4. Coherence change in relation to task performance

Coherence estimates in all pair-wise sites were calculated and compared between the resting and task performance. During the target-tracking task, coherence estimates increased in many pair-wise sites within sensory or motor area but also between sensory and motor areas. Coherence estimates increased significantly not only in the γ-range but also in α–β-frequency ranges. During wrist extension, the coherence changes in γ-range are not as significant as during the target tracking and threading, but the coherence estimates in the α–β-range increased in some pair sites. These data indicate that the coherence in the γ-range increases during task performances which demand more manipulative movement and more sensorimotor information processing. The coherence estimates in α–β-range increased during both the manipulative tasks and simple wrist extension, suggesting a common behavioral relevance of α–β-coherence to all task conditions.

4. Discussion

The present study showed that the power and coherence in γ-range increased in the sensorimotor cortex of human subjects when they performed manipulative visual motor tasks. γ-Oscillatory activity was overtly observed in three out of six subjects. For all six subjects γ-range power increased more significantly and in more sites during performance of manipulative visuomotor tasks, suggesting a functional role of γ-activity for the motor behavior. The appearance of γ-oscillations during task performance was accompanied with decreases in the activity at lower frequency range. α–β-Rhythms in human sensorimotor areas have been studied using electrocorticography, electroencephalography, and magnetic

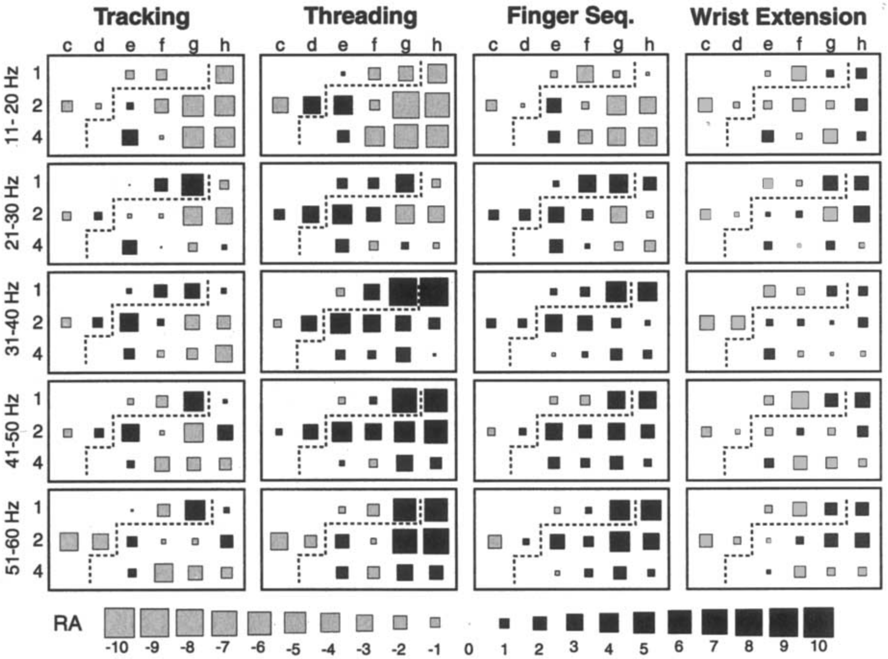

Fig. 4. Task-related changes in ECoG activity in subject RA. Squares represent Z-scores of power changes, relative to resting condition, during performance of the target tracking task, threading, finger sequencing, and wrist extension. The size of each square is proportional to the Z-score of the Mann–Whitney U-test for a given site and frequency range (scale at bottom). Positive and negative Z-scores denote increase and decrease, respectively, in power. Significance is $P = 0.05$ at $Z = 1.96$, $P = 0.01$ at $Z = 2.58$, and $P = 0.001$ at $Z = 3.27$. Black or open squares denote value of Z-score for an increase or decrease, respectively, in power during task performances relative to resting condition. The dashed line separates sensory and motor sites.

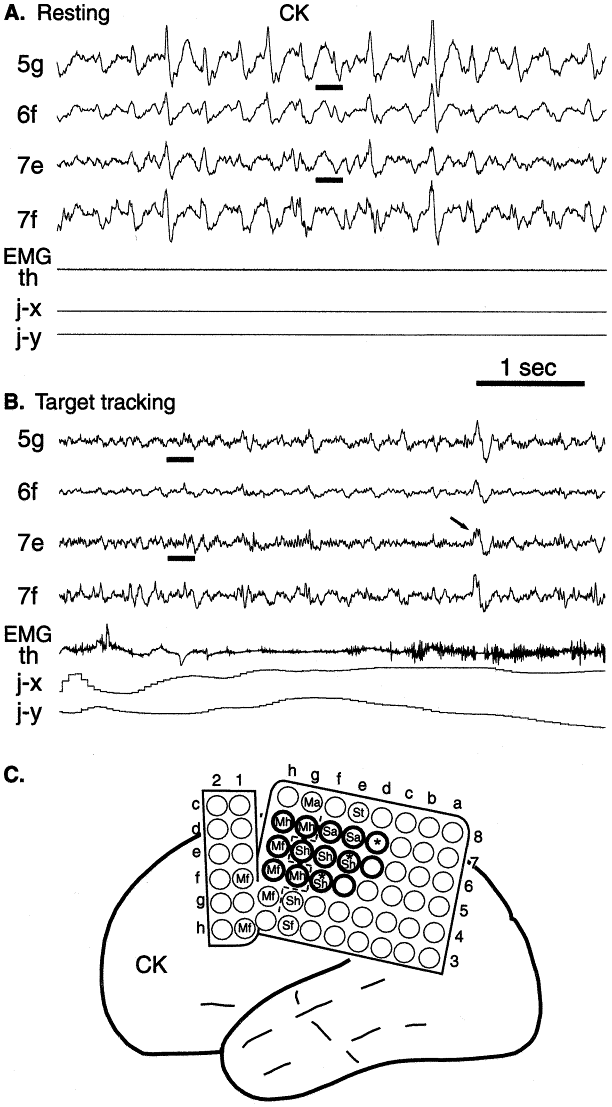

Fig. 5. Cortical activity of subject CK. Traces show ECoG from sites 5g, 6f, 7e, and 7f, EMG of thumb adductor, and x–y coordinates of the joystick. (A) At rest, synchronous interictal spike activity was evident at all sites. (B) During the target tracking, the epileptic discharges decreased and 40–50 Hz oscillatory waves appeared intermittently at sites 5g and 7e. (C) Schematic of recording electrode grid; convention as in Fig. 1C.

encephalography (Chatrian et al., 1959; Pfurtscheller, 1981; Tiihonen et al., 1989; Arroyo et al., 1993; Toro et al., 1994; Leocani et al., 1997; Classen et al., 1998). This so-called Rolandic wicket rhythm or μ-rhythm disappeared during movements of the contralateral limb. Increases in γ-power during motor tasks have been observed by spectral analysis of conventional EEG in human subjects (Spydell and Sheer, 1982; Spydell et al., 1979; Loring and Sheer, 1984; Pfurtscheller and Neuper, 1992; Pfurtscheller et al., 1993, 1994). One concern of spectral analysis of filtered EEG is the possibility that harmonics of α-activity may contribute to increases in γ-range power-

(Jurgens et al., 1995). In our study, all subjects showed decreases in α–β-range power and coincident increases in γ-range power during task performance, compatible with the observations in EEG studies by Pfurtscheller and Neuper (1992). Thus, the results suggest that γ-oscillatory activity is related to the performance of manipulative visuomotor tasks.

Task-related changes in γ-range activity have been investigated in sensorimotor cortex of monkeys. In some studies, oscillatory field potentials at 20–35 Hz were depressed when the subjects started movements (Sanes and Donoghue, 1993; Donoghue et al., 1998), similar to the blocking of the μ-rhythm in human subjects. In other cases, the oscillation in γ-band appeared more often during manipulative and exploratory behaviors (Murthy and Fetz, 1992, 1996a,b), or maintained precision grip (Baker et al., 1997). In the study by MacKay and Mendonça (1995) using a visually-guided reaching task with a preparatory period, β-range power was maximal during preparatory periods and minimal during reach performance, and γ-range power increased during the movement. Thus, these studies suggest that levels of α–β and γ-range activities are changed in different ways during manipulative motor tasks.

The result of CTA and cross-spectra in subject CK indicated that synchronization of γ-oscillations occurred between two separate sites in sensory and motor areas in a task-related way. The results from the coherence analysis in all pair-wise sites in the same subject indicated that synchronization of γ-range activity occurs within and between sensory and motor sites. Furthermore, the coherence analysis showed that coherence estimates increased in both α–β and γ-ranges during the manipulative task performance. Changes in the coherence estimates in γ-range were more vigorous during the manipulative tasks than during the simple wrist extension. The results indicate that synchronized γ-activity is task specific and related to performance of manipulative visuomotor task. In contrast, synchronization of α–β-activity may be related to a behavioral condition common to all motor tasks.

The roles of oscillatory activities and synchronization during perceptual motor tasks have been extensively debated. A study using ECoG in human brain showed no evidence of globally correlated activity related to behaviors (Menon et al., 1996). But other studies using EEG in human subjects showed that inter-regional coherence increased during perceptual motor tasks (Tremblay

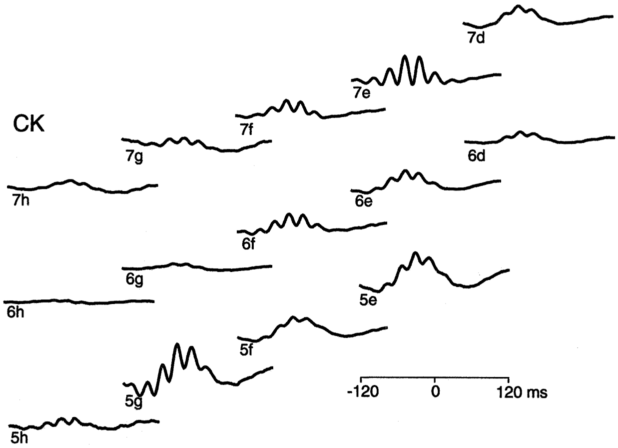

Fig. 6. CTAs of ECoGs recorded during target tracking in subject CK. Averages are aligned with triggers obtained from oscillatory cycles recorded at site 5g. Traces are positioned in accordance with the relative electrode locations in the subdural array (Fig. 5C). The averages show ECoG over 120 ms before and after the trigger.

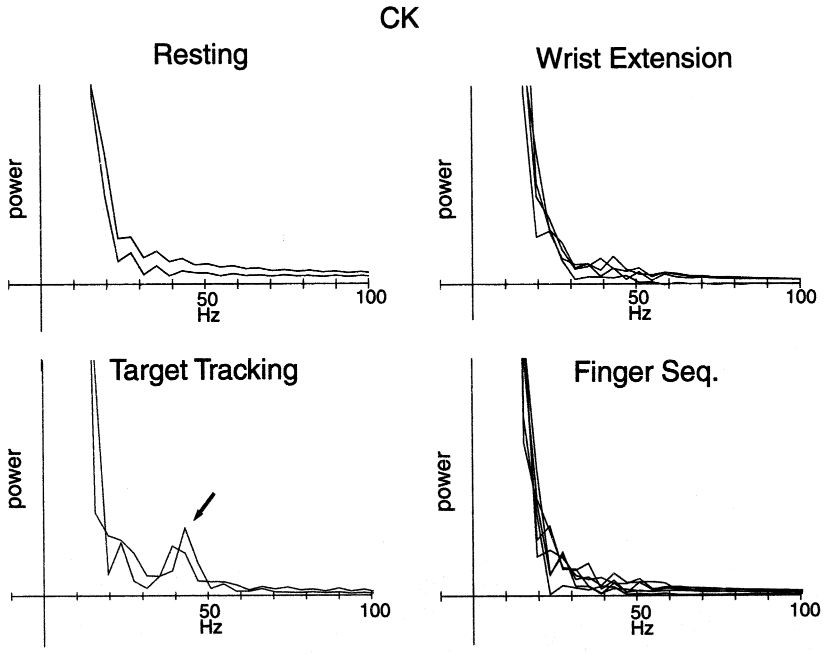

Fig. 7. Cross-spectra between sites 5g and 7e in subject CK, during rest, wrist extension, target tracking and finger sequencing. Note a peak in 40–50 Hz during the target tracking pointed by arrow.

et al., 1994; Classen et al., 1998; Rodriguez et al., 1999), and associative learning (Miltner et al., 1999). The results of these studies are compatible with the temporal binding hypothesis that has been supported in visual and olfactory systems. Synchronous γ-oscillations have been proposed to implement association of neuronal populations representing different information and integrate them into a unified percept. During performance of perceptual motor tasks, inter-areal binding has been extended to association between sensory and motor areas to facilitate perceptual motor information processing. In our study, the tracking task presumably required more integration of visual, proprioceptive and somatosensory information with ongoing motor activity, compared with the wrist extension, and showed increases in coherence estimates at higher significance level and in more electrode pairs, consistent with the association hypothesis. Oscillatory activities in motor cortex were reported to synchronize with EMG or motor unit activities in monkeys (Murthy and Fetz, 1992, 1996a; Baker et al., 1997) and in humans (Conway et al., 1995; Salenius et al., 1996, 1997; Halliday et al., 1998), indicating that oscillatory activities in motor cortex entrain motor unit activity. This suggests that coherent activities in sensorimotor cortex implement not only inter-regional interaction between sensory and motor cortices but also corticospinal interaction.

Another possible function of coherent activity may be related to increased attention or alertness. Tasks requiring information processing demand attention. The attentional level may be increased during manipulative tasks, such as the tracking and threading in the present study, during which the power and coherence in γ-range increased more vigorously compared with the simple wrist extension. This attentional hypothesis is supported by the observations that oscillatory activity appeared during increased alertness without any regular relation to the limb movements (Bouyer et al., 1981; Sheer, 1984; Murthy and Fetz, 1996a) and that the synchronization occurred in both task-related and unrelated neurons in the sensorimotor cortex (Murthy and Fetz, 1996b). Furthermore, other studies showed that the stimulation in brainstem reticular formation or ascending activation system could increase coherent γ-activity (Steriade et al., 1991, 1996; Munk et al., 1996). Clearly these hypotheses are not mutually exclusive. Since the tasks used to date have involved a combination of attention, co-ordination and sensorimotor integration, it remains for future studies to design tasks that better resolve these possible functions.

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