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Clinical Neurophysiology 110 (1999) 524–537

Increased gamma-range activity in human sensorimotor cortex during performance of visuomotor tasks

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Accepted 9 November 1998

Abstract

Objective: We documented changes in spectral power of human electrocorticograms (ECoG) during performance of sensorimotor tasks.

Methods: In 6 human subjects, ECoGs were recorded simultaneously from 14 subdural cortical sites in forearm sensorimotor cortex. The subjects performed 3 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 consisted of passive resting and active extension of the wrist. For each site the spectral power of the ECoG during these behaviors was computed for 5 10 Hz ranges between 10 and 60 Hz.

Results: All subjects showed power decreases in the range of 11–20 Hz and power increases in the 31–60 Hz range during performance of the visuomotor tasks, at sites in forearm sensorimotor cortex and adjacent areas. Simple wrist movements often produced little change in power. Three subjects showed episodes of explicit gamma oscillations during the visuomotor tasks. Different sites showed increases in gamma-range power for different tasks, indicating that the spatial distribution of the gamma activity is specific to the tasks. Cross-spectra showed that gamma activity could become synchronized between separate sites during particular tasks.

Conclusions: Synchronized gamma-range activity in human sensorimotor cortex increases with performance of manipulative visuomotor tasks, supporting the hypothesis that coherent gamma oscillations may play a role in sensorimotor integration or attention. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Oscillation; Gamma; Electrocorticogram; Sensorimotor cortex; Visuomotor task; Human

1. Introduction

Cortical activation associated with behavioral activity has long been known to involve desynchronization of low-frequency components of the resting electroencephalogram (EEG). More sensitive recordings have revealed that such activation can also involve increases in high-frequency activity in the gamma range (30–80 Hz) (Pfurtscheller and Neuper, 1992). The possible function of such gamma activity has been debated vigorously (Gray, 1994; Pantev et al., 1994; Singer, 1994; MacKay, 1997). Clear gamma oscillations in the mammalian brain were first observed in the olfactory system (Adrian, 1942), leading to extensive studies of the underlying cellular and physiological mechanisms. The olfactory bulb has been found to exhibit spatially coherent gamma range oscillation of the local field potential (LFP) whose amplitude contains odor-specific information (Bressler and Freeman, 1980; Freeman and Skarda, 1985; Freeman, 1991; Laurent et al., 1996). Studies in the visual system of monkeys have suggested that the spatial pattern of the gamma oscillations may be involved in processing behaviorally relevant information (Freeman and van Dijk, 1987; Kreiter and Singer, 1992; Livingstone, 1996). In the visual system, neuronal responses in the gamma frequency range became synchronized for sites in area 17 with similar orientation preference (Eckhorn et al., 1988; Gray et al., 1989), and could become synchronized between hemispheres and between striate and extrastriate areas (Eckhorn et al., 1988; Engel et al., 1991a,b; Roelfsema et al., 1997). The resultant temporal synchrony has been hypothesized to function as a binding mechanism for visual features and figure-ground separation (Engel et al., 1992). In the human visual system, gamma rhythms (25–50 Hz) induced by visual and auditory stimuli were recorded via depth electrodes in the calcarine cortex (Chatrian et al., 1960; Perez-Borja et al., 1961). However, these gamma waves were rather general and

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PII: S1388-2457(98)00064-9

Table 1
Summary of subjects (ECoG were recorded during performance of indicated tasks as well as during rest for all subjects)

Subjects	Age (years)	Sex	Neurological signs	Handedness	Recording side	Tasks performed			
						Target tracking	Threading	Finger sequencing	Wrist extension
B.R.	41	M	Normal	Right	Left	+			+
H.G.	23	M	Normal	Left	Right	+		+	
C.K.	12	F	Normal	Right	Left	+		+	+
R.A.	20	F	Diplegie (rt $<$ lt)	Right	Left	+	+	+	+
G.A.	16	F	Normal	Left	Right	+	+	+	+
H.L.	39	F	Normal	Right	Left	+	+	+	+

non-specific responses to various types of sensory stimulation.

Gamma-range oscillations also have been observed in the sensorimotor cortex of a variety of subjects in relation to motor behaviors. Murthy and Fetz (1992, 1996a,b) found episodes of widespread 25–35 Hz oscillations in monkeys performing exploratory limb movements; unit and field potential oscillations occurred synchronously in pre- and post-central cortex and bilaterally. Sanes and Donoghue (1993) observed field potential oscillations in monkeys performing an instructed delayed response; oscillations of 15–50 Hz occurred during the delay and decreased during the movement (Donoghue et al., 1998). MacKay and Mendonça (1995) observed broad-band increases in high-frequency power in parietal LFPs of monkeys during reaching. Baker et al. (1997) found evidence of oscillations in cortex and hand muscles of monkeys during a precision grip. Jasper and Penfield (1949) recorded 25 Hz electrocorticograms (ECoG) from the hand area of the precentral cortex in human subjects and observed that oscillations were blocked by movement of the contralateral finger. In cats, gamma oscillations in the sensorimotor cortex became very apparent when the animals were attentive and immobilized (Bouyer et al., 1981, 1987; Rougeul et al., 1979). Thus, most of these observations indicate that gamma oscillations in sensorimotor cortex may relate to attention or planning of movement, but have less reliable relation to execution of movement.

Using techniques developed to record human cortical activity simultaneously from multiple sites over a wide area, several investigators have studied the spatiotemporal patterns of activity. Coherent and distributed gamma oscillatory responses to auditory stimuli have been recorded via magnetoencephalography (Pantev et al., 1991; Ribary et al., 1991; Tesche and Hari, 1993). Scalp-recorded 40 Hz responses to auditory stimuli were highest when the subject paid attention to the stimuli (Tiitinen et al., 1993). The somatic sensorimotor system shows a decrease in 10 Hz power and an increase in 40 Hz power of the EEG during finger movement (Pfurtscheller and Neuper, 1992; Pfurtscheller et al., 1993). The spatial pattern of 40 Hz power could be differentiated between finger, toe and tongue movement by the topographical display of narrow-band power (Pfurtscheller et al., 1994). However, the spatial resolution of scalp-recorded EEG in humans is relatively limited compared with the resolution obtainable by direct cortical recording in animal studies; moreover, EEG signals are usually filtered with a narrow bandpass, risking the inclusion of harmonics of lower frequency (Jurgens et al., 1995).

Electrocorticography, which uses arrays of electrodes implanted subdurally, makes it possible to record potentials directly from the cortical surface at multiple sites simultaneously. This technique was used originally to localize the epileptic focus during surgical treatment of intractable epilepsy (Luders et al., 1987). The cortical sites can be functionally identified by electrical stimulation through the same electrodes (Ojemann, 1995). Recordings using the subdural electrodes with sufficiently wide band-pass filters can detect gamma-range activity with relatively high sensitivity. A previous study of the ECoG of two patients performing a sensory discrimination task produced little evidence for selective changes in power in particular frequency bands, and no evidence of globally correlated activity in the ECoG (Menon et al., 1996). In the present study, we used multichannel ECoG recording to investigate the presence and properties of gamma activity in the forearm and adjacent sensorimotor areas during performance of various visuomotor tasks.

2. Materials and methods

2.1. Subjects

Subjects were 6 patients with intractable epilepsy, two males and 4 females aged 12–41 years (Table 1). One subject (R.A.) exhibited diplegia (right $<$ left) but could use both hands and fingers for fine manipulation. None of the other 5 subjects showed any motor or sensory abnormality, including visual field deficits, on standard neurological examination. The subjects gave written informed consent to participate in the study.

The epileptic focus and functional sites were mapped with the use of subdural grid electrodes that were implanted for clinical indications over the fronto-parietal-temporal region contralateral to the side of seizures. The electrode array was composed of 64 stainless steel electrodes, each

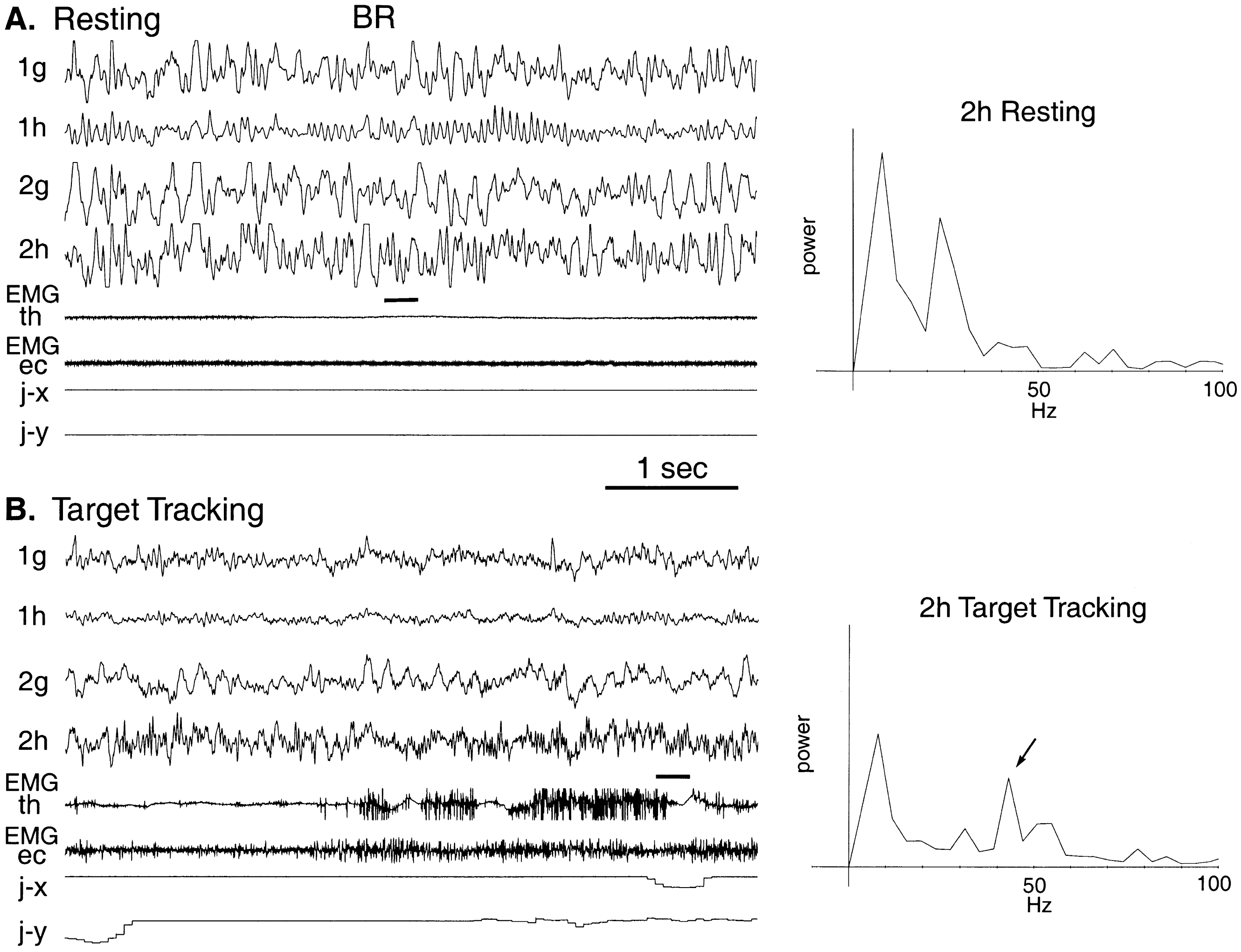

Fig. 1. Cortical activity of subject BR during rest (A) and target tracking (B). Traces from top down show ECoG at sites 1g, 1h, 2g and 2h (cf. Fig. 6), EMG of thumb adductor and extensor carpi radialis, and *x-y* coordinates of the joystick displacement. (A) During rest, intermittent 20–30 Hz oscillatory activity was observed in sites 1h and 2h. (B) During target tracking, 40–50 Hz oscillations were observed in site 2h. Right: power spectra of the signals from site 2h during times underlined in (A,B).

exposed to the cortex over a 2 mm diameter circle. The electrodes were arranged in a rectangular array, separated by inter-electrode distances of 1 cm, and embedded in a thin transparent silastic sheet. The subjects were monitored continuously for 7 days, during which ECoG and simultaneous video recording were obtained to localize the seizure focus prior to cortical resection, and the cortical function of sites was mapped by stimulation.

2.2. Functional mapping of sensorimotor cortex sites

Before the recording sessions we obtained functional maps of the cortical sites by delivering electrical stimuli through the implanted subdural electrodes. The electrical stimuli consisted of 60 Hz biphasic square pulses (1 ms/phase) in 2–3 s trains and were delivered through pairs of adjacent electrodes. Current intensity was set initially at 0.5–1.0 mA (peak-to-peak) and was increased in 0.5–1.0 mA steps to a maximum level of 11 mA, or until either a functional effect (motor, sensory, speech) or after-discharges occurred. 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) (including tongue and eyes), trunk (t) or leg (l).

2.3. Visuomotor tasks

During the performance of visuomotor tasks, the subjects were seated comfortably in bed with the back supported. Initial recordings were obtained while the subjects sat in a resting condition with their eyes open. A movement control was obtained while subjects ($n = 5$) performed a wrist extension task that involved active extension of the wrist joint for 2–20 s.

Visuomotor performance was tested by 3 tasks: target

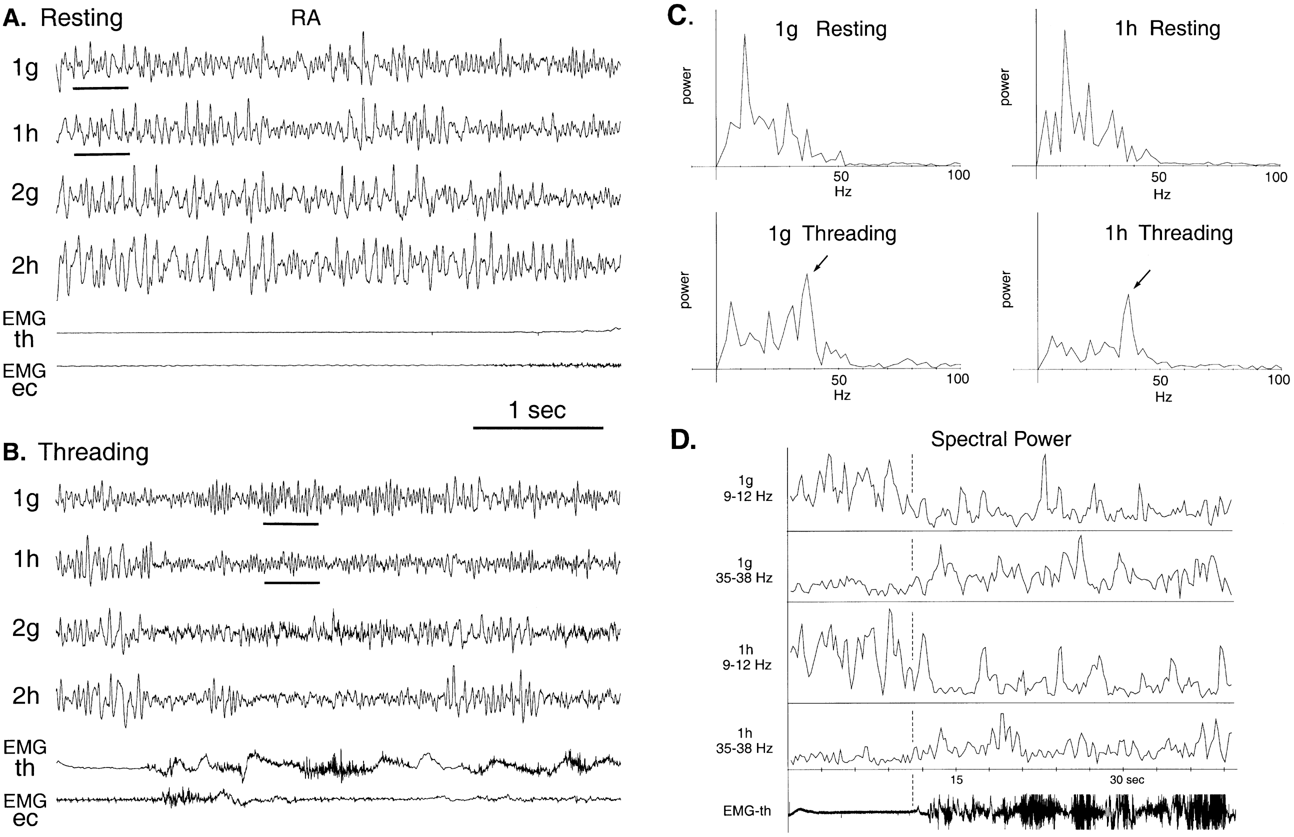

Fig. 2. Cortical activity of subject R.A. during rest (A) and needle threading (B). Traces show ECoG from sites 1g, 1h, 2g and 2h (cf. Fig. 9B) and EMG of thumb adductor and extensor carpi radialis. (A) During rest, ECoGs showed 10–30 Hz oscillations. (B) During threading, sites 1g and 1h exhibited intermittent 30–40 Hz oscillations. (C) Power spectra of the signals in sites 1g and 1h underlined in (A,B). (D) Running record of the power in low- and high-frequency bands for two sites, before and after onset of the threading task, as indicated by the EMG of thumb adductor (bottom). (Note: a similar running record of power over broader frequency bands for subject BR (site 2h) is illustrated in Fig. 7 of Murthy et al., 1994.)

tracking, threading and finger sequencing. In the target tracking task, the subjects ($n = 6$) followed a moving target on a video monitor with a cursor. The target was a 3 cm square (or, for the juvenile subject, a firecracker image) that moved at constant velocity across the screen, rebounding from the edges in random directions. Grasping a joystick with the entire hand or with the thumb and index fingers, the subject tried to keep the cursor within a bounded distance of the target for a brief period. After each successful tracking trial, the computer initiated a new target trajectory from a different position and incrementally titrated the speed of the target, the size of the target boundary, and the required tracking period. The initial parameters and their rate of titration were determined for each subject after several minutes of practice prior to recording. The recording session continued for 2–5 min, depending on the subject's level of fatigue. In the threading task, the subjects ($n = 3$) held a thread (~ 2 mm diameter) with one hand, picked up pieces of plastic tube (~ 1 cm long) with the other hand, and passed the thread through the tubes. In the finger sequencing task, the subjects ($n = 5$) made sequential pinches between the thumb and other fingers from index to little finger, and then in reverse order. They were allowed to watch their fingers during the performance.

The wrist extension, finger sequencing, and tracking tasks were performed with the hand contralateral to the ECoG recording side. In the bimanual threading task, the subjects were free to choose which hand would grasp the thread and which would pick up the tubes. These tasks require differing degrees of visuomotor integration, ranging from essential visuomotor interaction (tracking and threading) to negligible (sequencing) or none (extension).

2.4. Data collection

ECoGs were recorded from 14 sites, including the sites in forearm sensorimotor cortex identified by functional mapping and some adjacent sites. The ECoG was recorded relative to a Cz scalp reference. 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. With the use of a conventional EEG amplifier (Nihon Koden),

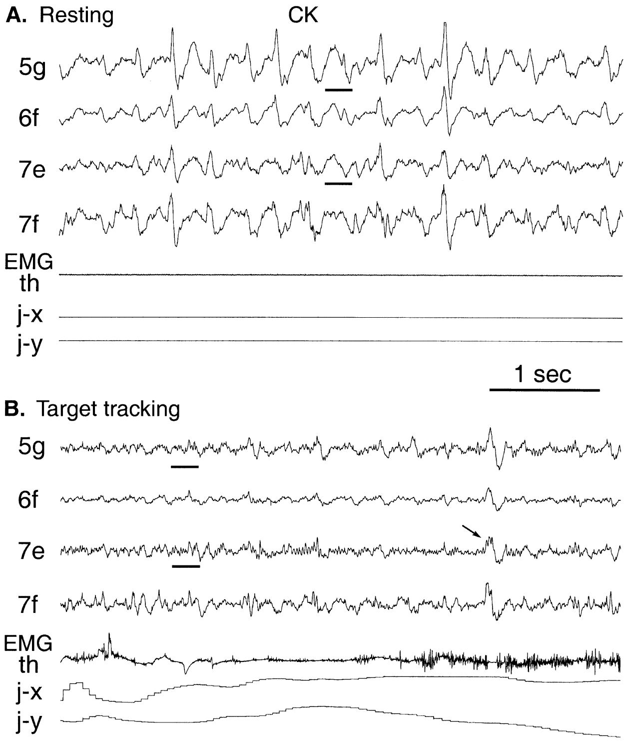

Fig. 3. Cortical activity of subject C.K. during rest (A) and target tracking (B). Traces show ECoG from sites 5g, 6f, 7e and 7f (cf. Fig. 8), EMG of thumb adductor, and *x*-*y* coordinates of the joystick. (A) At rest, synchronous interictal spike activity was evident at all sites. (B) During performance of the tracking task the epileptic discharges decreased and 40–50 Hz oscillatory waves appeared intermittently at sites 5g and 7e. Arrow indicates oscillation superimposed on epileptic spike.

the band-pass of the ECoG extended from 0.5 to 120 Hz (3 dB point; − 12 dB/oct) and the band-pass of the EMG was 5–500 Hz. The data were stored on cassette tapes in analog form (TEAC XR-9000) for off-line analysis. Movement onset for the performance of the tasks was estimated on the basis of EMG activity and, for the tracking task, on the basis of joystick movement.

2.5. Data analysis

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

For power spectrum analysis all the ECoG signals were digitized and stored with a 12 bit resolution at a sampling rate of 512 Hz. Analysis was performed on data sampled during different behavioral periods as follows: during the rest condition, a period of 12–65 s preceding task performance; the entire period of wrist extension (3–20 s) and finger sequencing (15–44 s); and the initial periods of joystick target tracking (40–55 s) and bimanual threading (44–56 s). Some data segments containing artifacts were excluded. 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 5 frequency bands: 11–20, 21–30, 31–40, 41–50 and 51–60 Hz. The significance of the power changes in each frequency band between the resting condition and each task was measured by means of the Mann-Whitney *U* test.

For the 3 subjects whose ECoG showed obvious gamma oscillation during the tracking task, we calculated cycle-triggered averages (CTA) and cross-spectra to document synchronization of oscillation between sites. For CTA, each oscillatory wave at one of these sites was used to generate triggers, and the signals at all sites were averaged for 2000 sweeps over a period of ± 120 ms aligned with the trigger. The cross-spectrum between two sites was calculated as the FFT of the cross-correlation function of the two signals. The cross-correlation function was calculated in an analysis period of 256 or 512 points during every 5 s for the resting and task conditions.

3. Results

3.1. Gamma oscillations during task performance

In 3 subjects, the appearance of gamma oscillations during performance of the visual motor tasks was obvious upon visual inspection of the ECoG signal. Representative ECoG records of subject B.R. during rest and performance of the tracking task are illustrated in Fig. 1 (for the relative locations of the recording sites see Fig. 6). During rest, the subject's ECoG exhibited activity in the range of 10–30 Hz, as seen at sites 1h and 2h. During performance of the target tracking task, this activity decreased and was replaced by increased activity in the range of 40–60 Hz. The shift in power is illustrated by the spectra for these behavioral conditions (Fig. 1, right). These spectra were calculated for selected samples, but the same shift is seen for the more comprehensive measures of the entire behavioral periods (Fig. 6).

A similar shift in power was evident during the threading task performed by subject R.A. The ECoG of this subject exhibited power predominantly in the 10–30 Hz range during rest (Fig. 2A). During performance of the bimanual threading task, sites 1g and 1h showed episodes of high-frequency activity (Fig. 2B). The power spectra computed for these episodes (Fig. 2C) indicate the appearance of sharp peaks in the 35–40 Hz band with the threading behavior. The continuous time course of the power changes is illustrated in Fig. 2D, which plots successive samples of power in the high- and low-frequency bands around the transition from rest to threading. These values show sustained reciprocal shifts in low- and high-frequency power with the task performance. Similar changes in average power for the task were also seen in neighboring sites (Fig. 9).

A third subject (C.K.) differed from the others in exhibiting widespread interictal spikes during rest (Fig. 3A). During the joystick tracking task, these epileptic spikes

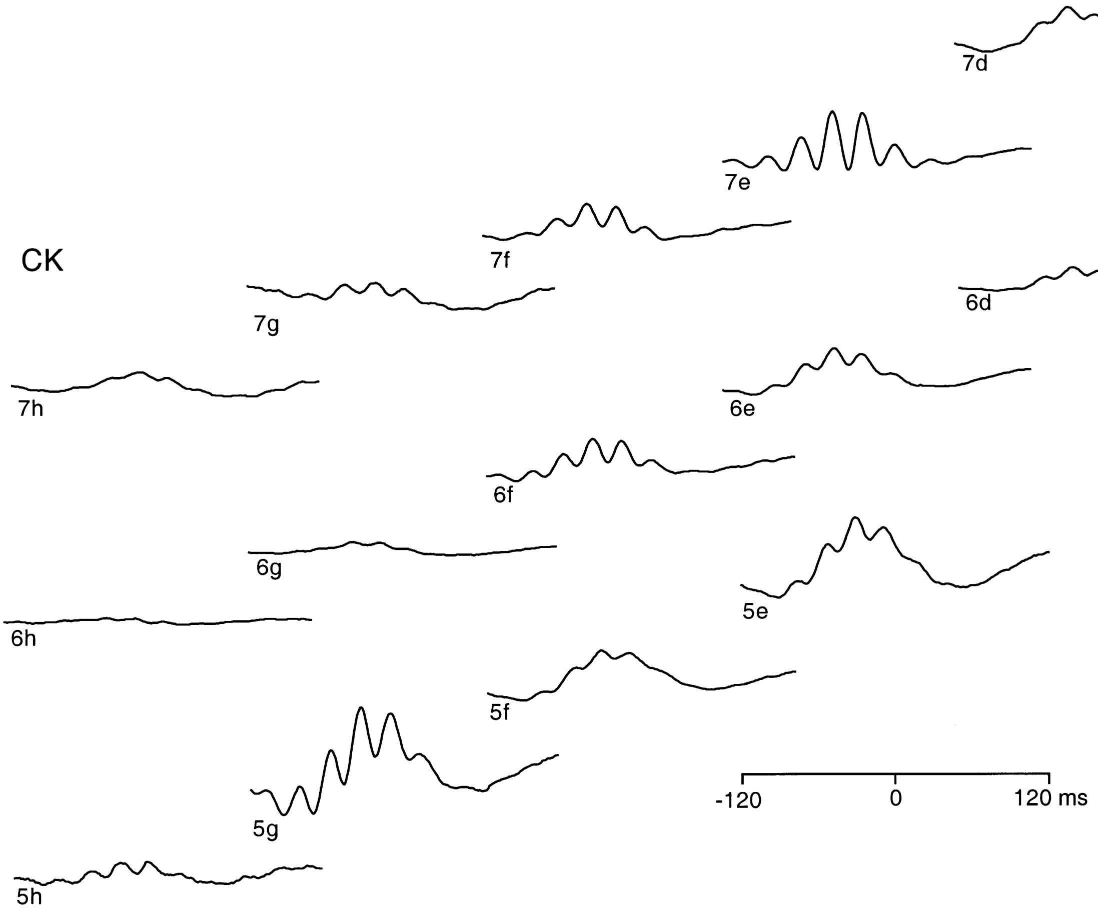

Fig. 4. Cycle-triggered averages of ECoGs recorded during target tracking in subject C.K. Averages are aligned with triggers obtained from oscillatory cycles recorded at site 5g. Traces are positioned in accordance with the relative electrode locations in the subdural array (cf. Fig. 8). The averages show ECoG over 120 ms before and after the trigger.

were reduced and intermittent episodes of 40–50 Hz oscillations occurred more often, as seen in records from sites 5g and 7e (Fig. 3B). Interestingly, the raw ECoG shows that oscillatory episodes could occur superimposed on epileptic spikes (Fig. 3B, arrow).

3.2. Synchronization of gamma oscillations

For the 3 subjects who showed obvious gamma oscillations in their ECoG, we documented the synchronization of these oscillations at separate sites by computing cycle-triggered averages (CTA) and cross-spectra. The CTAs show that oscillatory cycles occurred synchronously at different sensorimotor sites with negligible phase lag. This can be seen in the CTA of all 14 sites for subject C.K., during performance of the target tracking task (Fig. 4). The largest amount of synchronization appeared between sensory site 7e and motor site 5g, which triggered the CTAs. The cross-spectra between the spatially separated sites 5g and 7e showed a peak in the 30–40 Hz range during the tracking task, but not during either rest, wrist extension, or the finger sequencing task (Fig. 5). Similarly, for subject R.A. the cross-spectra between sites 1g and 1h showed a consistent peak in the 30–40 Hz range during the threading task, but not during rest or the tracking task (not shown). These data indicate that gamma oscillations at different sites became synchronized specifically during performance of particular tasks, but not under other behavioral conditions.

3.3. Changes in spectral power as a function of task conditions

To compare the changes in spectral power objectively for all 6 subjects and for all sites and frequency ranges, we performed Mann-Whitney *U*-tests between the resting condition and performance of the visuomotor tasks. The results are shown in Figs. 6–11. The Mann-Whitney *Z*-scores for each frequency range are represented by the sizes of squares at different cortical sites. Positive *Z*-scores (black squares) indicate an increase in power during task conditions, and negative *Z*-scores (open squares) indicate a decrease during task performance. The placement of the cortical grids is shown schematically for each patient. The recording sites are indicated with bold circles. The grid also labels the functionally identified sites as motor (M) or

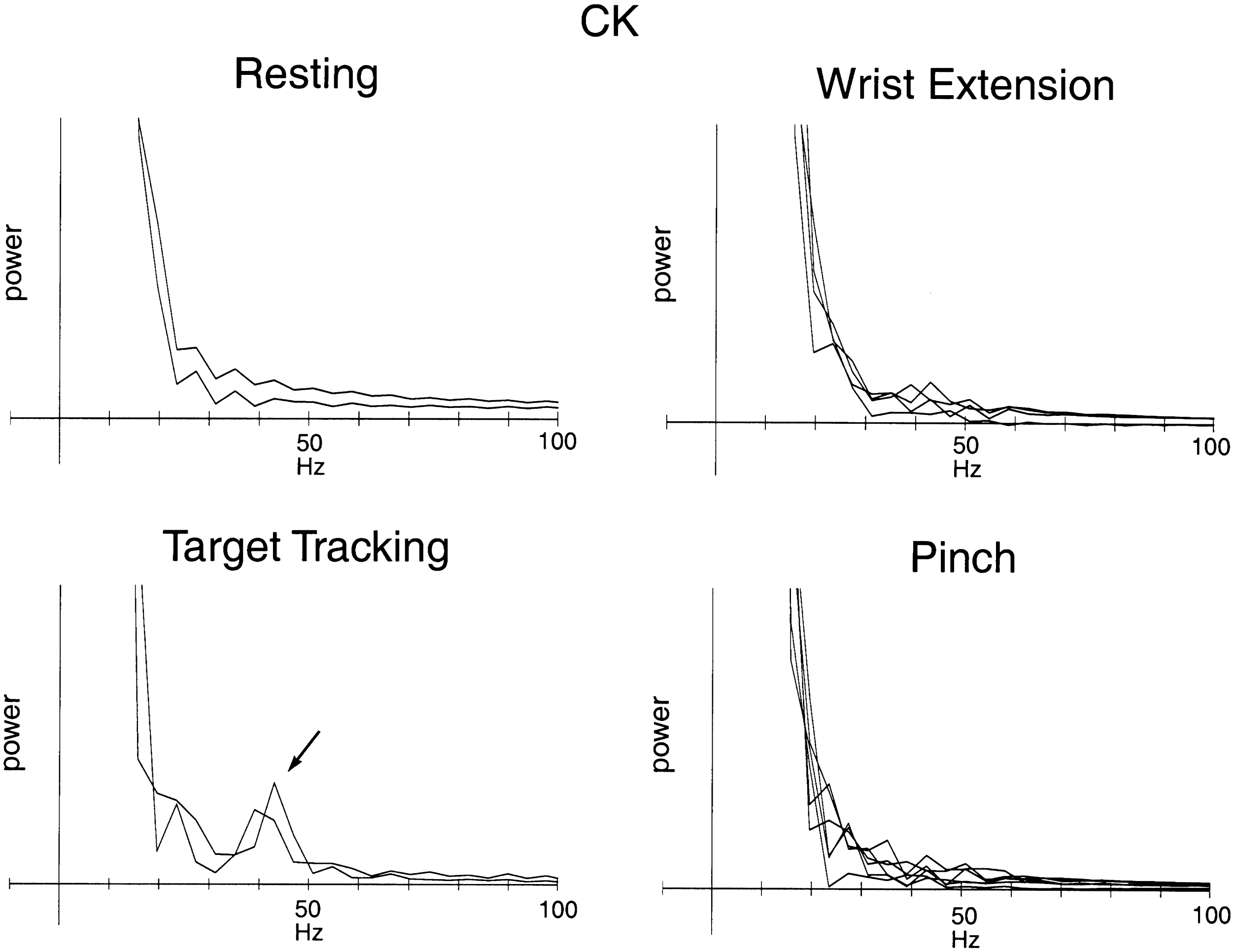

Fig. 5. Cross-power spectra between sites 5g and 7e in subject C.K. Cross-spectra were calculated as FFT of the cross-correlation of ECoG from sites 5g and 7e; correlogram window was 256 ms and superimposed traces represent spectra calculated during a 5 s period.

sensory (S), and indicates the somatic location of the response evoked. The dashed lines separate the S and M sites. Figs. 6 and 7 illustrate power changes for subjects B.R. and H.G. during performance of the target-tracking task relative to rest. Figs. 8–11 show the power changes relative to rest for subjects C.K., R.A., G.A. and H.L. during performance of the target-tracking task, threading, finger sequencing and wrist extension. All 6 subjects showed significant decreases ($P < 0.01$) in the 11–20 Hz range at sites in the forearm sensorimotor cortex and adjacent regions. All subjects also showed significant power increases in the gamma range, above 30 Hz during task performance. The transition between the low-frequency power decreases and the high-frequency increases occurred around 30 Hz for 4 subjects (B.R., H.G., C.K., H.L.) and around 20 Hz for the other two (R.A., G.A.). In several subjects, the anteromedial sites (largely motor and premotor) tended to show greatest increases in the lower gamma range of 20–40 Hz, whereas the posterior-lateral sites (sensory and post-sensory) tended to show greatest increases at higher frequencies of 40–60 Hz.

3.4. Spatially specific increases in gamma range power during different tasks

As shown in Figs. 9–11, the increases in gamma range power had different spatial distributions across the cortical sites, depending on which sensorimotor task was being performed. In subject R.A. (Fig. 9), the ECoG pattern during the finger sequencing task resembled that during threading, with gamma range power increases in sites 1g, 1h and 2e–h. In contrast, during the tracking task, only sites 1g and 2e showed significant increases in gamma range power. These patterns also differed from the distribution of weak changes associated with wrist extension.

The other two subjects who performed all 4 tasks also showed different spatial patterns of gamma range power increases during the different tasks. In subject G.A. (Fig. 10) the spatial patterns during threading, tracking and finger sequencing resembled each other in the 31–50 Hz range, all showing greater power increases than the pattern during wrist extension. However, the 3 sensorimotor tasks involved different spatial patterns in the other frequency ranges.

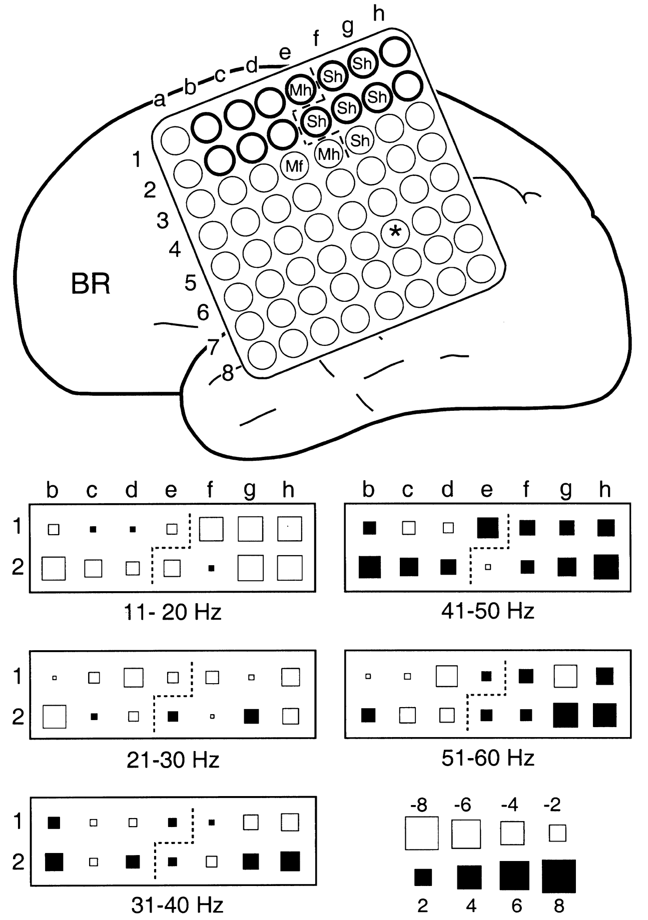

Fig. 6. Task-related changes in ECoG activity in subject BR. Schematic at top shows relative locations of subdural electrodes; dark circles indicate the analyzed recording sites. Functional mapping by direct electrical stimulation identified some sites as motor (M) or sensory (S); lowercase letters indicate somatic location: hand (h), arm (a), face (f), trunk (t) and leg (l), in this and subsequent figures. Sites with an asterisk (*) were identified in long-term recordings as sites where epileptic activity first appeared at onset of seizures. The matrices of squares at bottom show results of the Mann-Whitney *U*-test of the powers in each frequency range at each site, comparing the tracking task with resting conditions. The size of each square is proportional to the *Z*-score of the test for a given site and frequency range (scale at lower right). Significance in this and subsequent figures 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) in power during the tracking task relative to resting condition. The dashed line separates sensory and motor sites. The same format is used in Figs. 7–11.

Similarly, in subject H.L. (Fig. 11), increases in the 31–50 Hz range showed comparable spatial distributions in the tracking and threading tasks, which differed from those in the sequencing task at posterior sites; again, all 3 differed from the weaker pattern during wrist extension.

3.5. Relation to sites of epileptic activity

In 4 subjects, recordings included cortical sites designated as ‘epileptic,’ namely, sites that showed the first epileptic activity at onset of seizures during long-term recording. Epileptic sites represented 7–21% (mean 14%) of the recording sites in these 4 subjects. Across all frequency ranges for the 3 complex motor tasks, the data provided 45 comparisons between epileptic and immediately adjacent sites. Of these 45 comparisons, 26 (58%) exhibited smaller changes in power at the epileptic sites. For each sensorimotor task, there was one frequency range where all subjects had smaller changes at epileptic sites: 21–30 Hz for tracking and sequencing and 30–41 Hz for threading. Wrist extension, which generated fewer overall changes in gamma frequencies, did not show smaller changes at epileptic sites, and no frequency ranges showed consistent changes with extension in all subjects. The fact that epileptic sites showed fewer changes with complex sensorimotor tasks is further evidence that epileptic brain tissue is less functional than normal. Over all subjects, epileptic sites represented 10% of the total number of recording sites ($n = 8/84$). Thus, 90% of the recordings were from non-epileptic tissue.

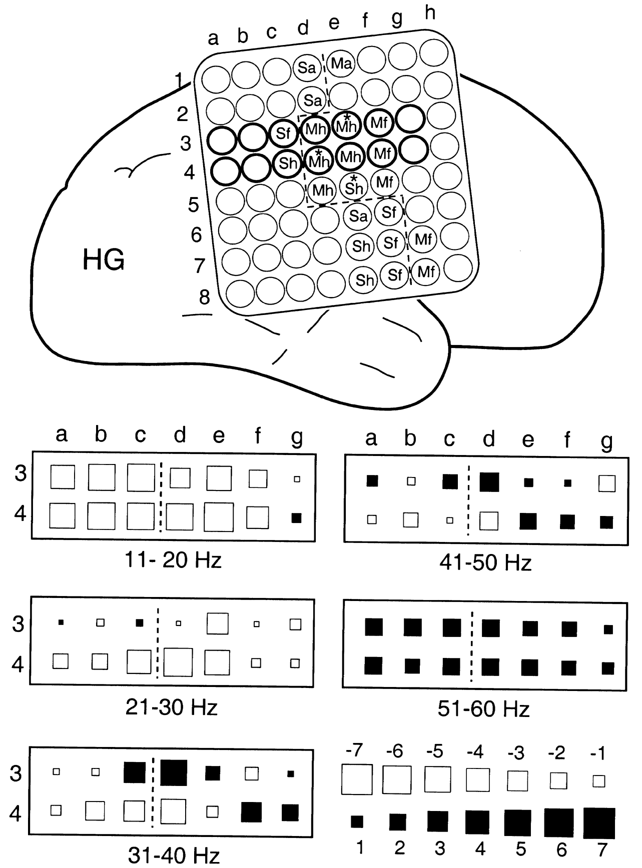

Fig. 7. Electrode grid and task-related changes in ECoG activity in subject H.G. Squares represent the Mann-Whitney *Z*-scores of power changes during the tracking task relative to resting conditions.

4. Discussion

4.1. Gamma activity related to visuomotor task performance

This report is the first to show increased gamma activity

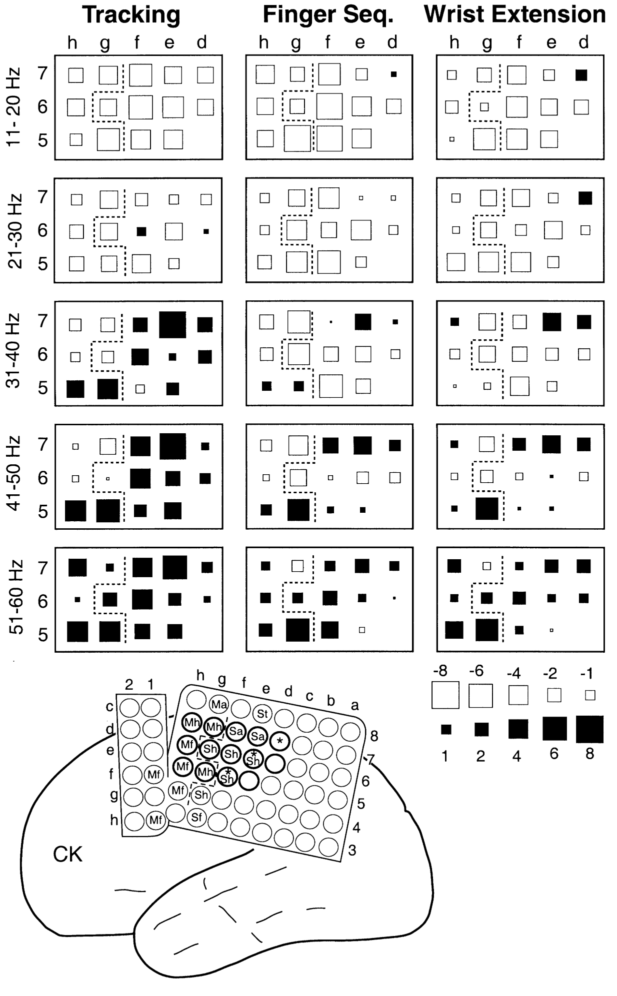

Fig. 8. Task-related changes in ECoG activity in subject C.K. Squares represent power changes, relative to resting conditions, during the tracking task, finger sequencing and wrist extension. Schematic of recording electrode grid at bottom; convention as in Fig. 6.

in broadly filtered ECoG recorded in human sensorimotor cortex, during performance of specific visuomotor tasks. Previous work has documented decreases in low-frequency power with movements. Jasper and Penfield (1949) first reported 25 Hz oscillations in the ECoG in human precentral cortex, which disappeared during contralateral finger movements. The alpha-beta rhythm in human sensorimotor areas has been studied with the use of electrocorticography, electroencephalography, and magnetic 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 mu rhythm disappeared during movements of the contralateral limb; this ‘blocking of the mu rhythm’ is a motor example of event-related desynchronization. A similar desynchronization of ECoG in the alpha range has been observed to occur specifically at language sites during performance of language tasks in human subjects (Fried et al., 1981; Ojemann et al., 1989). Such desynchronization was confirmed recently, and found to be replaced with higher-frequency activity (Crone et al., 1994).

Increases in gamma power during motor tasks have been revealed by spectral analysis of conventional EEG recorded over the scalp (Spydell et al., 1979; Spydell and Sheer, 1982; Loring and Sheer, 1984; Pfurtscheller and Neuper, 1992; Pfurtscheller et al., 1993, 1994). One concern about the spectral analysis of filtered EEG, however, is the possibility that harmonics of alpha activity may contribute to apparent increases in gamma range power (Jurgens et al., 1995). In our study, all 6 subjects showed decreased power in the alpha-beta range, concomitant with increased power in the gamma range during task performance, similar to results obtained in EEG studies (Pfurtscheller and Neuper, 1992). In half of our subjects this shift was obvious in the raw ECoG.

A recent study using similar grid recordings of ECoG found no evidence for increases in gamma power in subjects discriminating the strength of a somatosensory stimulus (Menon et al., 1996). Although some somatosensory sites did exhibit task-related decreases in low-frequency power, the spectra showed no evidence for sustained increases in gamma power. This difference may be related to the difference in the tasks. Whereas their two subjects performed a discriminative reaction time task (Gevins et al., 1994), our subjects performed various manipulative tasks in a continuous manner. The significance of the behavioral conditions is demonstrated by the fact that even within our subjects, different tasks generated different patterns, and negligible increases in gamma power occurred with simple wrist movement.

Task-dependent changes in gamma activity have also been investigated in non-human primates. Oscillations in field potential at 20–35 Hz have been documented in the sensorimotor cortex of monkeys during performance of various motor tasks. In some cases these oscillations decreased during movement (Sanes and Donoghue, 1993; Donoghue et al., 1998), similar to the drop in the alpha-beta band activity of human subjects. In other cases, the oscillations occurred more often during reaching movements (MacKay and Mendonça, 1995; Murthy and Fetz, 1992, 1996a,b) or during maintained precision grip (Baker et al., 1997). Another study reported broad-band increases in power, in monkeys performing a visual reaction-time task (Bressler et al., 1993). Again, these diverse observations may be related to the specific behavioral conditions, as well as other experimental differences.

4.2. Spatial patterns of the gamma oscillation depend on the tasks

Electrocorticography provides simultaneous recordings of activity from multiple cortical sites with high spatial and temporal resolution. Moreover, the sites can be located relative to functionally identified motor and sensory sites.

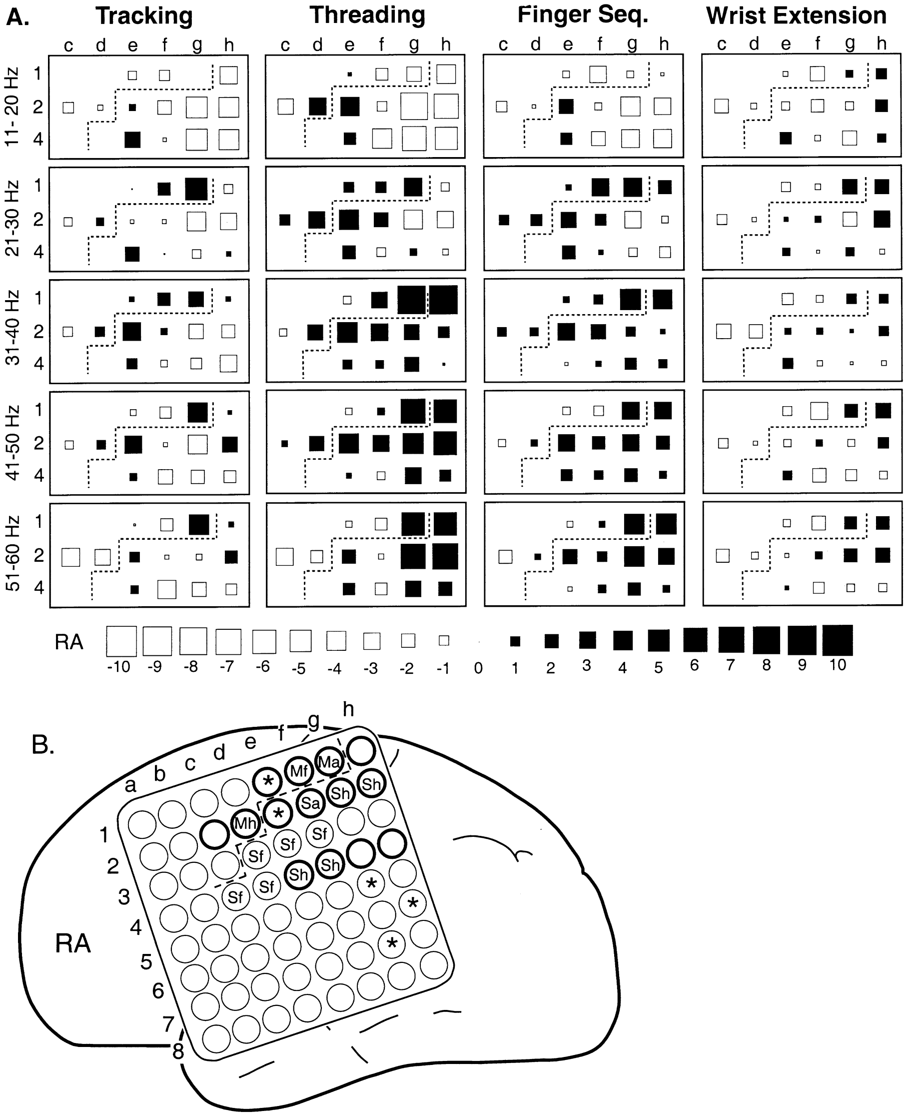

Fig. 9. (A) Task-related changes in ECoG activity in subject R.A. Squares represent the *Z*-scores of power changes, relative to resting conditions, during performance of (left to right) the target tracking task, threading, finger sequencing, and wrist extension. (B) Schematic of electrode grid.

These records showed concomitant increases in gamma power in both motor and sensory sites in all 6 subjects. The spatial patterns of the gamma activity accompanying performance of the 3 sensorimotor tasks were clearly different from patterns associated with simple wrist extension (Figs. 9–11). Moreover, the different tasks could also be associated with different patterns. Similarly, in sensory systems the spatial pattern of gamma range LFP activity has been reported to be stimulus specific: patterns in the rabbit olfactory bulb and cortex were related to inhaled odors (Freeman and Skarda, 1985; Freeman, 1991), and patterns of gamma activity in the monkey visual cortex depended on the visual stimuli (Freeman and van Dijk, 1987). Thus, one might infer that the spatial patterns of such gamma activity reflect the processing of sensory information. In the present study, it was not possible to identify any clear correlations between the instantaneous spatial pattern of gamma range power and either movement parameters or sensory input (Fig. 2D). However, the mean spatial pattern tended to depend on the sensorimotor task. In subjects G.A. and H.L., for example, the spatial patterns during threading and target tracking resembled each other more strongly than the pattern during finger sequencing. Threading and tracking both involve continuous visuomotor integration, while finger sequencing involves primarily proprioceptive-motor integration. In subject R.A., however, spatial patterns during finger sequencing resembled those during threading, and both patterns differed from those during target tracking. In this case, the salient factor may be that target tracking is strongly controlled by visual input, while the other two tasks involve self-paced sensorimotor activity. These observations suggest that the spatial pattern of the gamma range power may be related to the motor and sensory processing required for execution of the tasks.

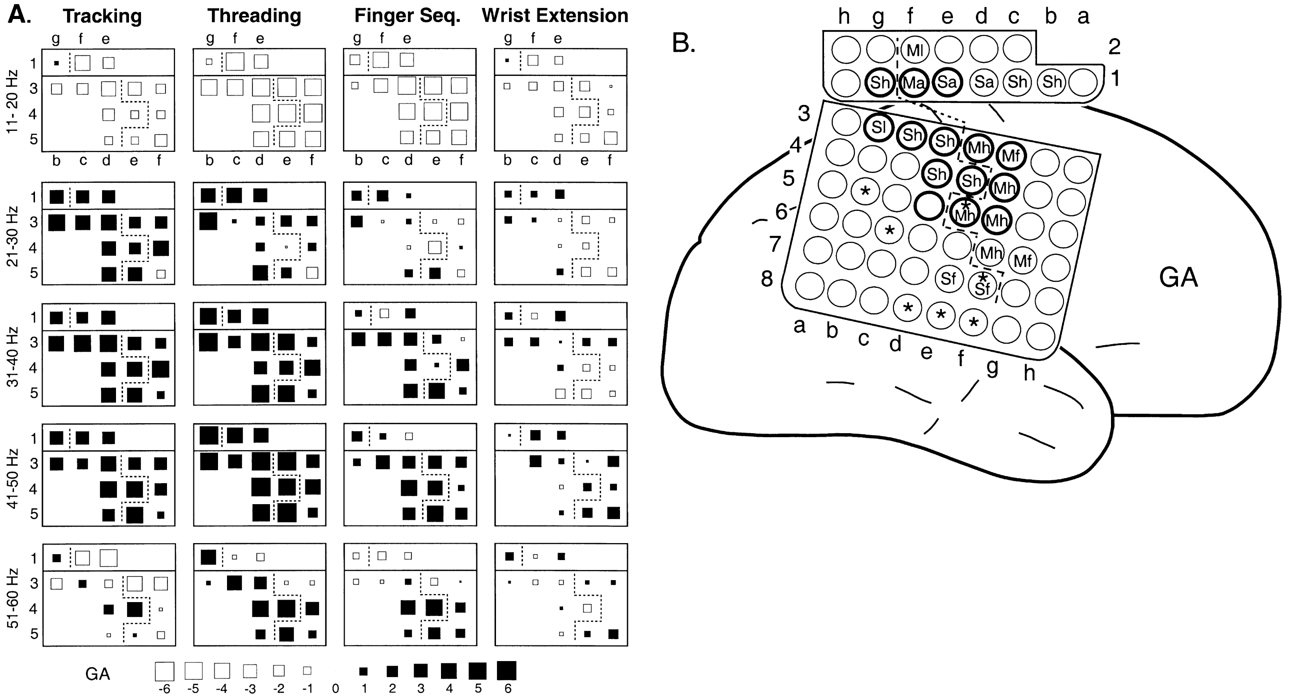

Fig. 10. (A) Task-related changes in ECoG activity in subject G.A. Squares represent the *Z*-scores of power changes, relative to resting conditions, during performance of the tracking task, threading, finger sequencing, and wrist extension. (B) Schematic of electrode grid. Note that two sets of recording sites were separated by a gap.

4.3. Synchronization of the gamma oscillation

We found that gamma oscillations at separate sites often became synchronized. The cortical extent of the synchronous activity was more restricted in these human recordings than previously found in monkey sensorimotor cortex (Bressler et al., 1993; Murthy and Fetz, 1992; Murthy and Fetz, 1996a; Sanes and Donoghue, 1993). Synchronous oscillations were most widespread in subject C.K., who also showed the most extensive distribution of synchronous interictal spiking. The relatively strong and widespread synchrony in this subject may be a consequence of the sustained facilitation of synaptic connections generated by her incessant interictal activity. Nevertheless, the cross-spectra in subject C.K. showed that coherence occurred in a task-specific manner, in agreement with other human studies (Leocani et al., 1997; Classen et al., 1998).

4.4. Possible function of gamma activity

The observed increases in synchronized gamma oscillations during specific sensorimotor tasks have implications for their possible functional role. At one extreme, the null hypothesis would consider oscillations to be simply an epiphenomenon of general increases in cortical excitability associated with behavioral activity. In this view, transient oscillations may result if a critical level of cortical instability is exceeded. One argument against this hypothesis reasons that widespread spurious oscillations and the concomitant entrainment of many neurons into periodic firing (Murthy and Fetz, 1996b) should interfere with their normal interactions and their rate-coded functions. However, many epileptic patients exhibit widespread synchronous interictal activity that does not seriously disrupt their behavior. Indeed, recent evidence suggests that distributed patterns of cortical activity mediating different behaviors may be superimposed (Arieli et al., 1996). This would indicate that the cortex could support some degree of epiphenomenal oscillations without disruption of normal function.

Beyond the null hypothesis one can also consider two functional roles for widespread gamma activity. The ‘binding hypothesis’ suggests that such synchronous activity may facilitate associations between cortical neurons that individually represent different aspects of a given ‘gestalt,’ for example, in visual perception of a figure against a ground (Singer, 1994). According to this hypothesis, synchrony serves as a temporal code to bind the cells representing features of an object (Engel et al., 1992). In the cat visual system, the synchronization of gamma oscillations has been proposed to mediate such temporal binding within and between the visual areas (Eckhorn et al., 1988; Engel et al., 1991a,b; Gray et al., 1989, 1992; Roelfsema et al., 1996, 1997). In the present study, the tracking, threading and sequential fingering tasks all required integration of visual, proprioceptive and somatosensory information with ongoing motor activity. Indeed, the subjects showed similar spatial patterns of gamma activity while performing tasks

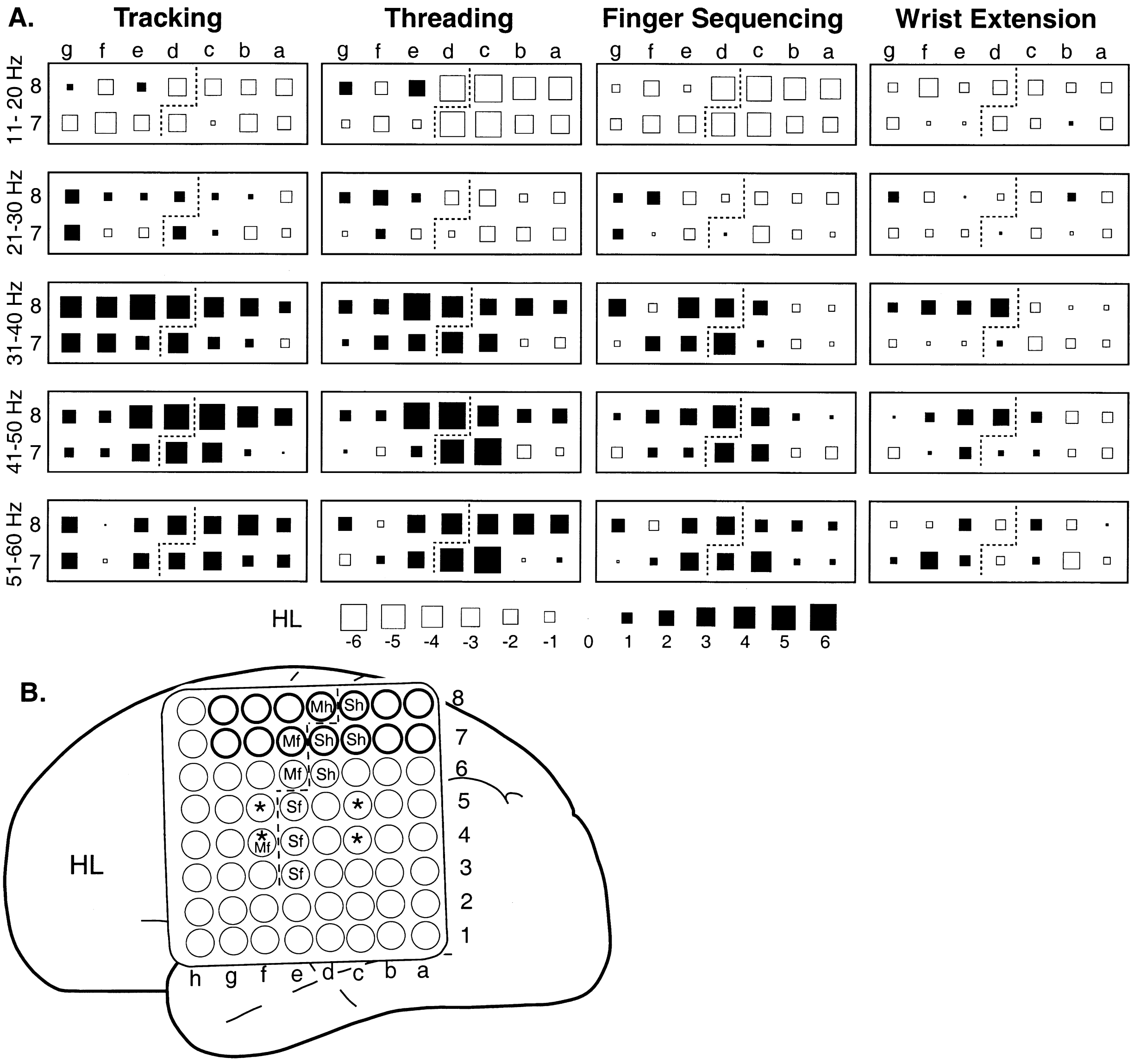

Fig. 11. (A) Task-related changes in ECoG activity in subject H.L. Squares represent the *Z*-scores of power changes, relative to resting conditions, during the tracking task, threading, finger sequencing, and wrist extension. (B) Schematic of electrode grid.

that involved similar sensorimotor requirements. These observations would be consistent with the hypothesis that synchronization of gamma oscillations may function to bind sensorimotor information necessary to perform specific tasks. However, these tasks also involve increased levels of concentration, so the gamma activity could also reflect mechanisms of increased attention. This third hypothesis is supported by evidence that oscillations appear under conditions of increased alertness (Bouyer et al., 1981; Bouyer et al., 1987; Murthy and Fetz, 1996a; Sheer, 1984). The attentional hypothesis is further consistent with the fact that gamma oscillations could be evoked by stimulation of the brain-stem reticular system (Munk et al., 1996; Steriade et al., 1991). The properties of the increased gamma activity documented in this study are ultimately compatible with each of the 3 hypotheses above, but have different implications for each. Further studies could be designed to help resolve these possibilities (Murthy and Fetz, 1996b; MacKay, 1997).

Acknowledgements

We thank Dr. Nancy Temkin and Mr. Heracles Panagiotides for help with statistical analysis, Mr. Jonathan Garlid for help with instrumentation, and Ms. Kate Elias for editorial help. This work was supported in part by the Human Frontiers Science Program, the Japan Foundation for Aging and Health, and grants NS12542 and RR00166 from the National Institutes of Health.

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