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Timing and Localization of Movement-Related Spectral Changes in the Human Peri-Rolandic Cortex: Intracranial Recordings

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Event-related spectral power (ERSP) was measured from intracranial EEG and used to characterize the time-course and localization of the Rolandic mu rhythms in 12 patients during the delayed recognition of words or faces (DR) and the discrimination of simple lateralized visual targets (LVD). On each trial, the subject decided whether to make manual response (Go) or not (NoGo). ERSP increased on both Go and NoGo trials in peri-Rolandic regions of all subjects with a peak latency of ~330-ms poststimulus and duration of 260 ms during the DR task. The peak of this ERSP increase preceded movement by ~300 ms. All subjects produced a subsequent movement specific ERSP decrease of peri-Rolandic mu rhythms (starting ~90 ms before the average reaction time) with an peak latency of ~800 ms and duration of ~520 ms. The LVD task produced bilateral movement-selective readiness potentials and reproduced the movement-specific late ERSP decreases seen in the DR task (strongest from 7–24 Hz). Furthermore, the LVD task demonstrated that the late movement-related ERSP decrease is larger for the contralateral hand. However, the LVD task did not consistently reproduce the early ERSP increase seen in the DR task. Movement-related ERSP decreases were widespread, occurring in pre- and post-Rolandic as well as primary-motor, supplemental motor, and cingulate cortical regions. Other cortical areas including frontal, temporal, and occipital regions did not show movement-related ERSP changes. Peri-Rolandic ERSP decreases in mu rhythms correlate with the generation of a motor command. The early increases in mu may reflect a transient state of motor inhibition just prior to motor execution. © 2001 Academic Press

Key Words: **event related spectral power; EEG; motor cortex; evoked rhythms; mu rhythm.**

INTRODUCTION

The Rolandic cortex of a relaxed human subject exhibits neuro-electric oscillations around 10 to 20 Hz known as the "mu rhythm." These oscillations can be detected noninvasively at the scalp with EEG (Jasper and Penfield, 1949; Gastaut, 1952) and outside the head with MEG (Magnetoencephalography: Salmelin and Hari, 1994b). Mu activity is minimally affected by visual stimulation, and can therefore be distinguished both spatially and functionally from the occipital alpha rhythm (Chatrian *et al.*, 1959; Koshino and Niedermeyer, 1975). Tactile stimulation, motor preparation, and voluntary movement all transiently suppress the mu rhythm (Chatrian *et al.*, 1959; Pfurtscheller and Neuper, 1992). Subdural electrode grids have also shown that the mu rhythm can be blocked by contralateral face and arm movements, passive movements of contralateral arm, and by ipsilateral arm movements (Arroyo *et al.*, 1993). In short, Rolandic mu rhythms are most prevalent during the absence of movement and therefore have often been interpreted as the resting rhythm of the Rolandic cortex.

There are two opposing viewpoints that endeavor to describe how the brain sequences motor information. The first proposes elementary neural processors that operate serially. In this conception, a processor is activated only upon the completion of processing by the preceding steps (Donders, 1969; Sternberg, 1969; Miller, 1982, 1983). Thus, the motor cortex would become active only after all contributing cortical regions had produced a movement plan and activity in motor cortex would exclusively reflect the execution and delivery of the motor plan. An alternate viewpoint speculates that the motor cortex gradually accumulates evidence and that a movement response is generated once this evidence reaches a critical threshold (Eriksen and Schultz, 1979; McClelland, 1979; Coles *et al.*, 1985; Smid *et al.*, 1991). This approach proposes that, unlike the discrete steps in serial processing, the output of a neural processing unit is continuously available to all subsequent or current processes.

The evidence reviewed above suggests that the desynchronization of the mu rhythm may be helpful in understanding the timing and location of the neural

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processes involved in motor planning and execution in human subjects. Most previous studies of Rolandic mu rhythms have been based on electrical potentials (or magnetic fields) recorded at the scalp (Salmelin and Hari, 1994b; Salmelin and Hari, 1994a; Stancak and Pfurtscheller, 1996; Pfurtscheller and Neuper, 1997). In comparison to EEG/MEG recorded outside the head, intracranial EEG (iEEG) allows for greater accuracy in defining the frequency content and timing of neuroelectric signals. Scalp electrodes record EEG from a relatively large volume of cortex and sample neuronal activity from many millions of cells (Nunez, 1981). Electrical potentials are smeared by the high impedance skull intervening between the signal source and the recording electrode contacts. The signals may be refocused, but only by assuming that they are generated by a single or few dipoles. However, the validity of such assumptions are unknown and may lead to mislocalization. For example, extended generator sources, when recorded with scalp EEG, can produce the illusion of generators deeper than their true location (Ary *et al.*, 1981; Coles and Rugg, 1995). Additionally, temporal asynchronies and spatial misalignments within the large region sampled in a scalp recording can result in the cancellation of the net signal, and thus the contributions of small regions may be obscured.

This study examines intracranial EEG data collected from a unique human subject population immediately prior to and during volitional movement tasks. All subjects suffered from pharmacoresistant epilepsy and were implanted with depth electrodes for seizure monitoring. In order to assess the temporal and spectral characteristics of peri-Rolandic rhythms we analyzed the data with a variant of the spectral power measure. Averages of time-varying event-related spectral power (ERSP) have previously revealed stimulus induced oscillatory EEG activity roughly time-locked but not specifically phase-locked to stimulus events (Makeig, 1993; Jokeit and Makeig, 1994; Klopp *et al.*, 2000). These measures were compared to the traditional event-related potential (ERP), a measure that is insensitive to oscillations that are not specifically phase locked to the stimulus. By applying both measures it is possible to observe both phase locked and non-phase locked event related alterations of the intracranial EEG as recorded from within cortical structures known to participate in motor planning and execution.

METHODS

Participants

Intracranial EEG (iEEG) was analyzed from peri-Rolandic cortex of 12 subjects. Subjects suffered from pharmacoresistant complex partial epilepsy and were candidates for surgical therapy (Chauvel *et al.*, 1996). Depth electrodes were recommended only if noninvasive measures were inadequate to identify the seizure focus. Subjects gave fully informed consent and were monitored by institutional review boards.

Electrodes and Localization

Depth electrodes were 0.8 mm in diameter, blunt-tipped, and had 5, 10, or 15 recording contacts. Each contact was 2.0 mm in length, and adjacent contacts were separated by 1.5 mm. EEG was analyzed from a total of 532 contacts. This included 173 iEEG contacts located within peri-Rolandic, cingulate and pre-motor cortex that passed artifact rejection requirements (Tables 1 and 2 and Fig. 1). For the delayed recognition task, waveforms were digitized every 6 ms at 12-bit resolution for 1200 ms beginning 120 ms before stimulus onset. In the lateralized visual discrimination task waveforms were digitized every 3 ms at 12-bit resolution for 768 ms, beginning 50 ms prior to stimulus onset. Recordings in both tasks were unipolar and referenced to the tip of the nose. Targeted MRI and angiography were used to localize electrode placement (Talairach and Tournoux, 1988; Musolino *et al.*, 1990). Given the three-dimensional folded structure of the Rolandic fissure and the orientation of the electrodes (perpendicular to the midline sagittal plane) it was possible for a single electrode probe to pass both through pre- and postcentral regions. At least four depth probes (1B, 2A, 7A′, and 9C) recorded activity from cortex posterior to the central sulcus as well as more medially in cortex anterior to the central sulcus.

As a result of limitations imposed by intracranial human studies the tasks presented here were not optimized for motor studies. In particular, most recordings in the DR task were ipsilateral to hand movement. The one exception was subject 7 who had premotor recordings in both hemispheres. In this subject left and right recordings were combined in the analyses. All subjects in the LVD task had peri-Rolandic recordings that were both contralateral and ipsilateral to hand movement. Additionally, subjects 7 and 9 had simultaneous bilateral peri-Rolandic recordings. Probe targets were determined on clinical grounds for reasons unrelated to the experimental paradigms.

Behavioral Tasks

Subjects performed one of two motor tasks (subject 7 performed both). In both tasks, the subject reclined on a bed with his or her back elevated and maintained a fixed gaze on a target. Stimulus presentation was controlled and behavioral responses were monitored for latency and accuracy by a microcomputer. The DR task required declarative recognition memory and a “go, no-go” motor decision/response. Stimuli were either faces or words, which were presented in separate blocks (140 to 280 trials per condition). Of the seven

TABLE 1

DR Task: List of Subjects, Completed Tasks (Word and/or Face), Response Hand, Implanted Regions, Number of Electrode Contacts, and Corresponding Coordinates (Talairach and Tournoux, 1988)

		DR task			Talairach coordinates				
Subject	Probe	Words	Faces	Response hand	*x*	*y*	*z*	Region	Electrode contacts
1	A	X	X	R	34 to 59	−5	21	R Inf Post-C	3
	B_1				27 to 56	−19	43	R Sup Post-C	3
	B_2				6 to 13	−19	43	R Cing G	2
2	A_1	X	X	R	41 to 52	−8	13	R Inf Pre-C	3
	A_2				59 to 63	−8	13	R Inf Post-C	2
3	A	X	X	R	31 to 52	−1	16	R Inf Pre-C	5
	B				4 to 36	12	44	MFG to R SMA	5
4		X	X	R	45 to 59	7	7	R Inf Pre-C	3
5			X	R	32 to 59	−4	19	R Inf Pre-C	6
6			X	R	41 to 63	3	12	R Inf Pre-C	8
7	A'_1	X		L	−9 to −20	−21	62	L Sup Pre-C	3
	A'_2				−26 to −40	−21	62	L Sup Post-C	4
	B′				−11 to −49	10	51	MFG to L SMA	12
	C				1 to 47	4	49	MFG to R SMA	14

Note. Inf Post-C, inferior post central gyrus; Sup, superior; Cing G, cingulate gyrus; MFG, middle frontal gyrus; Pre-M, premotor; SMA, supplementary motor area.

subjects, four performed the DR task with both face and word stimuli while the rest performed with only one or the other stimulus type (Table 1).

Faces were shown as color slides on a back projection screen and words on a video monitor. Stimuli were presented every 3 s for a duration of 300 ms. Faces subtended a visual angle of 5.5° horizontal by 8.3° vertical. The face stimuli were photographs of previously unfamiliar young adults of European descent who lacked beards or mustaches. Words subtended a visual angle of 1.2 to 1.5° horizontal by 0.4° vertical. They were sampled from both low and high lexical frequency lists ((Halgren *et al.*, 1994a, b) for complete methodological details). Prior to task performance, subjects were familiarized with a subset of the stimuli in training runs and instructed to finger press a button only in response to familiar stimuli (50% targets). Subjects responded with their dominant hand, which in all cases but one was the right hand. A feedback tone was presented 1200 ms after stimulus onset indicating the accuracy of the response and limiting the response period. Subject 7 suffered from right-sided hemiparesis and therefore could only respond with the left hand.

During the lateralized visual discrimination task subjects manually responded to target stimuli (25%) and refrained from responding to nontarget stimuli (75%). The stimuli (+ and O) subtended 0.5° of visual angle and were counterbalanced across sessions as to which symbol was the target and which was the nontarget. The stimulus symbols were presented in black

TABLE 2

LVD Task: List of Subjects, Response Hand, Implanted Regions, Number of Electrode Contacts, and Corresponding Coordinates (Talairach and Tournoux, 1988)

			Talairach coordinates				
Subject	Probe	LVD task response hand	*x*	*y*	*z*	Region	Electrode contacts
7	A'_1	L	−9 to −20	−21	62	L Sup Pre-C	3
	A'_2		−26 to −40	−21	62	L Sup Post-C	4
	B′		−11 to −49	10	51	MFG to L Sup Pre-M	12
	C		1 to 47	4	49	MFG to R Sup Pre-M	14
8′		L & R	−28 to −59	4	18	L Inf Pre-C	10
9	A′	L & R	−7 to −42	−12	50	MFG to L Sup Pre-C	12
	B		8 to 50	−7	38	Cing G to R Sup Pre-C	12
	C_1		8 to 22	−30	52	Cing (SSA) to R Sup Pre-C	5
	C_2		29 to 45	−30	52	R Sup Post-C	6
10		L & R	17 to 58	−7	23	R Inf Pre-C	13
11		L & R	31 to 63	0	8	Insula to R Inf Pre-C	6
12		L & R	39 to 57	−4	22	R Inf Pre-C	3

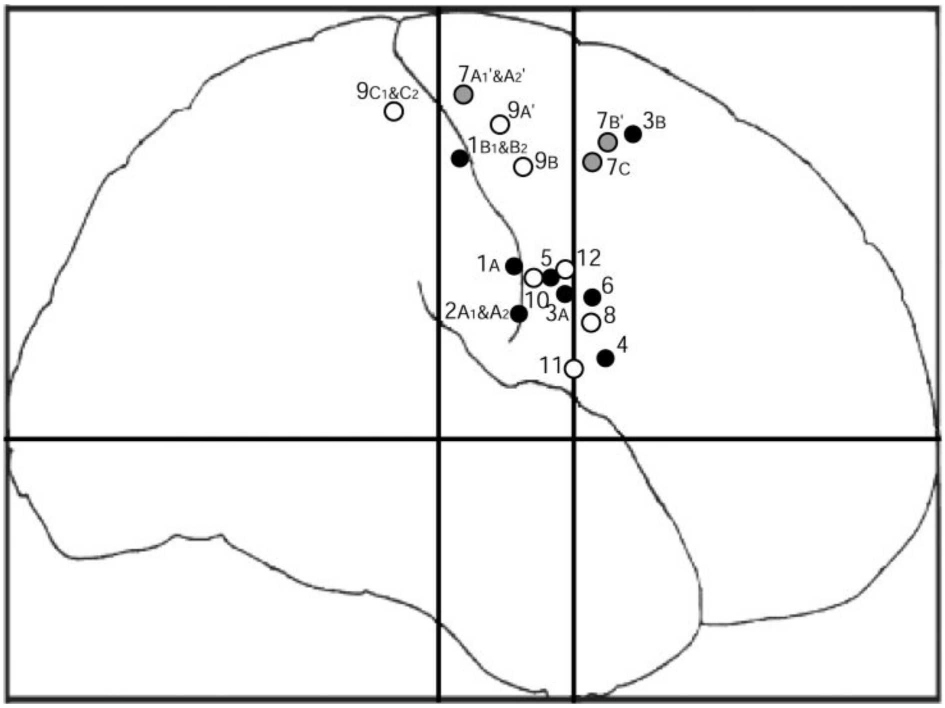

FIG. 1. Saggital brain schema illustrating implanted regions. Lateral points of entry of multicontact probes recorded during the DR task are solid circles. Empty circles indicate lateral points of entry sites recorded during the LVD task. The gray circles indicate depth probe sites in the single subject that performed both tasks. Electrode probes were positioned perpendicular to the midline. Both left and right probes are plotted here on the right hemisphere in the proportional Talairach system (1988). An apostrophe after the probe number (i.e., A′) indicates that the probe was implanted in the left hemisphere. Upper probes extend to the midline. Most probes sample different regions along their lateral to medial trajectory.

against a white background. A given session consisted of 384 trials, and for each trial a stimulus was presented for 150 ms on a video monitor. Individual trials were separated by 1500 ms. Subjects maintained a visual fixation on a central point (an x), and pressed a response key with their left or right thumb whenever a target stimulus appeared. Halfway through a session, subjects rested and alternated response hand. Each patient participated in one to three sessions depending on their availability ((Clarke *et al.*, 1999) for complete methodological details).

Analysis

All spectral and statistical analyses were performed with the S-Plus software package (Mathsoft, Inc.) on a Silicon Graphics Origin-200 computer. Trials contaminated by epileptiform EEG spikes, eye movements, or other large transients were excluded. On average 6% of the electrode contacts were rejected as located in epileptogenic areas, and in the remaining areas 14% of the trials were rejected on amplitude criteria.

ERSP was measured as the square root of power and baseline-normalized in four frequency bands. Due to differences in the lengths of prereference and total epoch recordings between the DR and the LVD tasks, different frequency bands were used in the analysis. In the DR recordings the frequency bands included theta (5–6 Hz), alpha (7–12 Hz), beta (13–24 Hz), and gamma (25–45 Hz). A sliding window was used with EEG epochs (each 198 ms long for theta band measures, 180 ms for alpha and beta, and 36 ms for gamma) to attain a higher temporal resolution. That is, ERSP was recalculated after shifting the window an increment smaller than the analysis epoch length. This increment was 60 ms for the theta band, 30 ms for alpha, and beta and 12 ms for gamma.

In the LVD task the frequency bands included alpha (8–12 Hz), beta^1 (13–18 Hz), beta^2 (19–24 Hz), and gamma (25–45 Hz). The size of the sliding window was 128 ms for alpha, beta^1, and beta^2 and 40 ms for gamma. The sliding increment was 30 ms for alpha, 15 ms for beta^1 and beta^2, and 6 ms for gamma. To compute the ERSP, each epoch was analyzed using an unnormalized discrete Fourier transform. For individual trial-based ERSP (iERSP) these calculations were performed on the EEG from each trial, and then averaged across trials for a given subject, task, electrode contact, and trial type. For average-based ERSP (aERSP), the EEG was first averaged across trials for a given subject, task, electrode contact, and trial type, and then the ERSP calculations were performed on this averaged EEG (i.e., the ERP). The resulting values were normalized to show percentage change from baseline.

Statistics

Analytic statistical measures (z scores) were corrected for multiple measures by multiplying probability outputs by a factor of the number of tests performed for each iEEG contact times the percentage by which adjacent iEEG epochs overlapped. Given that subsequent probability measures were not independent this correction is expected to slightly underestimate statistical significance. $P < 0.01$ was taken as a minimal threshold for significance.

RESULTS

Delayed Recognition (DR) Task

The average percentage of correctly answered trials was 87 ± 2% for faces and 91 ± 2% for words. The average reaction time was 626 ± 79 ms to identify repeating faces and 637 ± 67 ms for repeating words.

All subjects displayed early (200–460 ms) significant iERSP increases compared to baseline in at least one peri-Rolandic iEEG contact (Fig. 2, top). The average peak latency of this iERSP increase was at 330 ms, with an average duration of 260 ms. Early iERSP increases appeared in both movement and nonmovement conditions and were seen in all frequency bands (i.e., from 5 to 45 Hz). There was a tendency for the early ERSP increase to be strongest in the range of 7–12 Hz, and it was somewhat larger in the movement condition in four of the seven subjects. However, the early increase in iERSP was overall nonspecific and weaker than the subsequent movement associated iERSP decrease described below.

All subjects showed significant poststimulus iERSP decreases within the 7–12 and 13–24 Hz frequency ranges ($P < 0.01$) in pre- and postcentral areas (Fig. 2, bottom). Cingulate, premotor, and supplementary motor areas showed similar activity. Average onset of the iERSP decrease ranged from 300 to 750 ms and peaked at an average 800 ms poststimulus onset, i.e., at the time of the motor response (button press). On average the peak of iERSP decrease was 530 ms later than that of the early iERSP increase. Unlike the early iERSP increase, the late iERSP decrease was highly specific for the movement condition. The movement specific iERSP decrease was clearly significant in all but one subject. Only word stimuli elicited a movement specific iERSP decrease in subject 2, and face stimuli produced a late, nonspecific iERSP decrease.

The 13–24 Hz delayed recognition iERSP time course and location is illustrated for all recorded sites in a representative individual (subject 7) with peri-Rolandic recordings contralateral and ipsilateral to the hand movement (Fig. 3). The movement condition shows a distinct iERSP decrease during the button press phase of the task. In contrast, the nonmovement condition has an ERSP decrease of lesser amplitude. Moreover, movement-associated iERSP decreases are focally located in bilateral premotor and peri-Rolandic regions. Data recorded from other cortical areas, including frontal, occipital, and parietal regions lack similar movement-specific characteristics. Movement associated iERSP decreases are preceded by a weak iERSP increase in the nonmovement condition and a slightly stronger and focal early iERSP increase in two electrode contacts from the left postcentral Rolandic region during the movement condition. Given that similar iERSP fluctuations occur across multiple iEEG contacts in this example the iERSP decrease is probably generated from a distributed source while the iERSP increase may be generated by a more anatomically constrained source in postcentral cortex.

Event related potentials were averaged across multiple representative electrode contacts from all subjects. The resulting multi-subject average ERP did not yield a clear distinction between movement and nonmovement conditions (Fig. 4). In both conditions a negative potential appears from 360–600 ms. In contrast, an average of iERSP results from the same set of electrode contacts produced distinctive temporal characteristics that were consistent across subjects and specific to the task condition (Fig. 5). This across subject average of normalized iERSP values shows an early nonspecific iERSP increase in the lower frequency bands (5–12 Hz) followed by a clear movement-associated iERSP decrease beginning around 450 ms. The late iERSP decrease generally appeared across a wide frequency range (5–45 Hz), but is most prevalent in the higher frequency bands (13–45 Hz) (Fig. 2, bottom, and Fig. 5).

It is important to note that the ERSP calculated from the average trial, i.e., the ERP (aERSP), failed to yield any task specific changes (Fig. 5). This was because the task-related broadband decrease in spectral power was only apparent with respect to the prestimulus baseline, and activity in this period was lost in the averaging procedure.

Lateralized Visual Discrimination (LVD) Task

In the LVD task the number of rejected trials ranged from 3 to 17% with an average of 13% per subject. There was an average of only 1.8% errors made (targets missed 2.4% of the time, and false alarms to nontargets occurred 1.3% of the time).

All subjects produced a strong, late, movement-specific iERSP decrease. This iERSP decrease began before and continued after the motor response and was largest when the contralateral hand performed the motor response (Fig. 6). An across subject average of

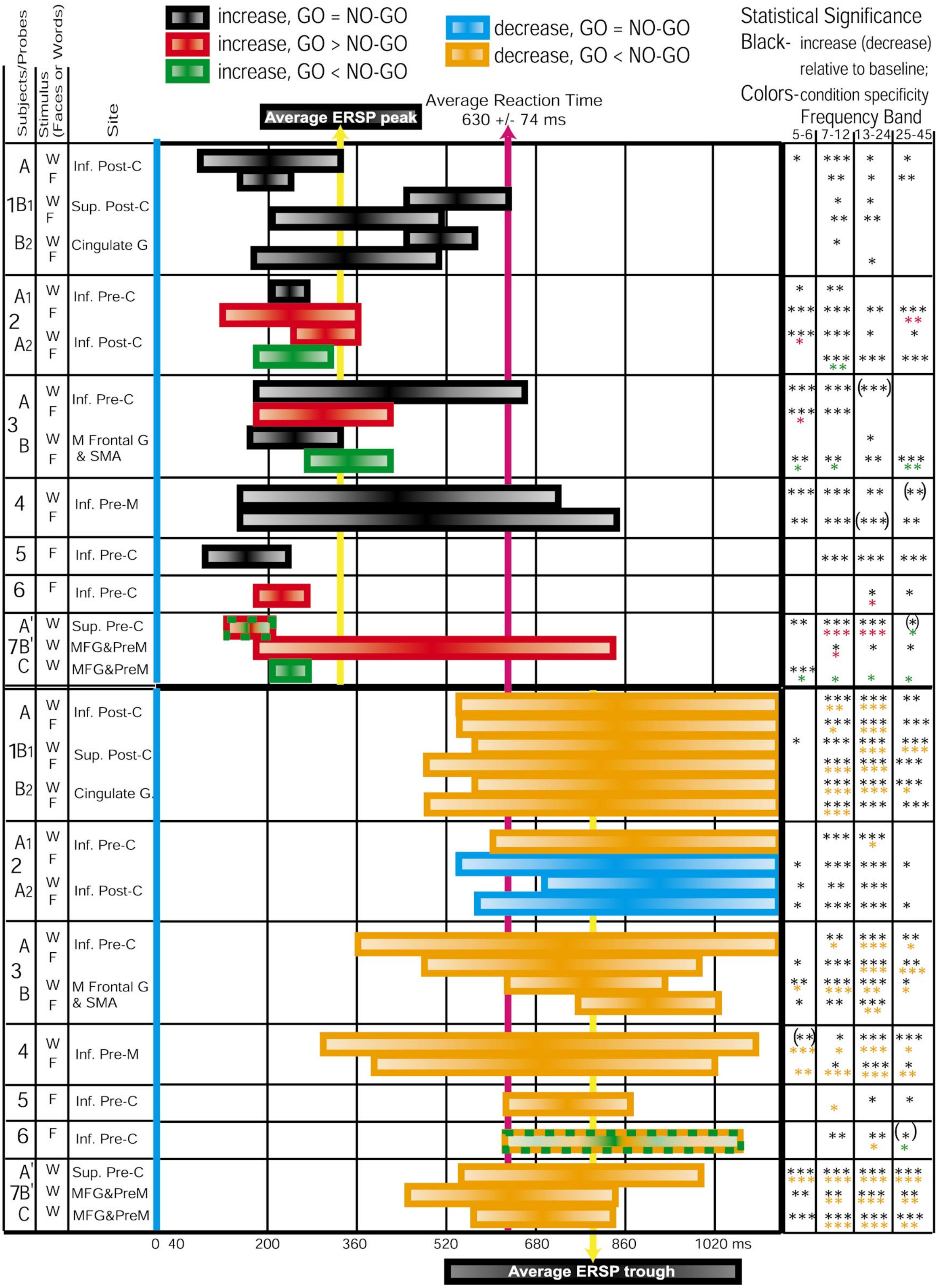

FIG. 2. Early increases and late decreases in the DR peri-Rolandic ERSP. Results are shown for individual subjects, regions and tasks for periods that maintained significant changes in iERSP relative to baseline in at least one contact. Statistics are shown for both the occurrence of an iERSP increase (top half) and iERSP decrease (bottom half) as well as for specificity of the task condition (color coded). Statistical significance is measured between baseline and subsequent time epochs and noted as $*P < 0.01$, $**P < 0.0001$, $***P < 0.000001$. ERSP increases are seen in the peri-Rolandic region of all subjects with an average peak latency of 330 ms poststimulus (upper yellow arrow) and duration of 260 ms that were usually movement nonspecific (black bars). The peak of the ERSP increase preceded movement by an average of 300 ms. All subjects produced a movement specific ERSP decrease of peri-Rolandic mu rhythms with an average peak latency of 800 ms (lower yellow arrow) and duration of 520 ms (orange bars). The average reaction time occurred at 630 ms ± 74 ms after the stimulus onset (red arrow).

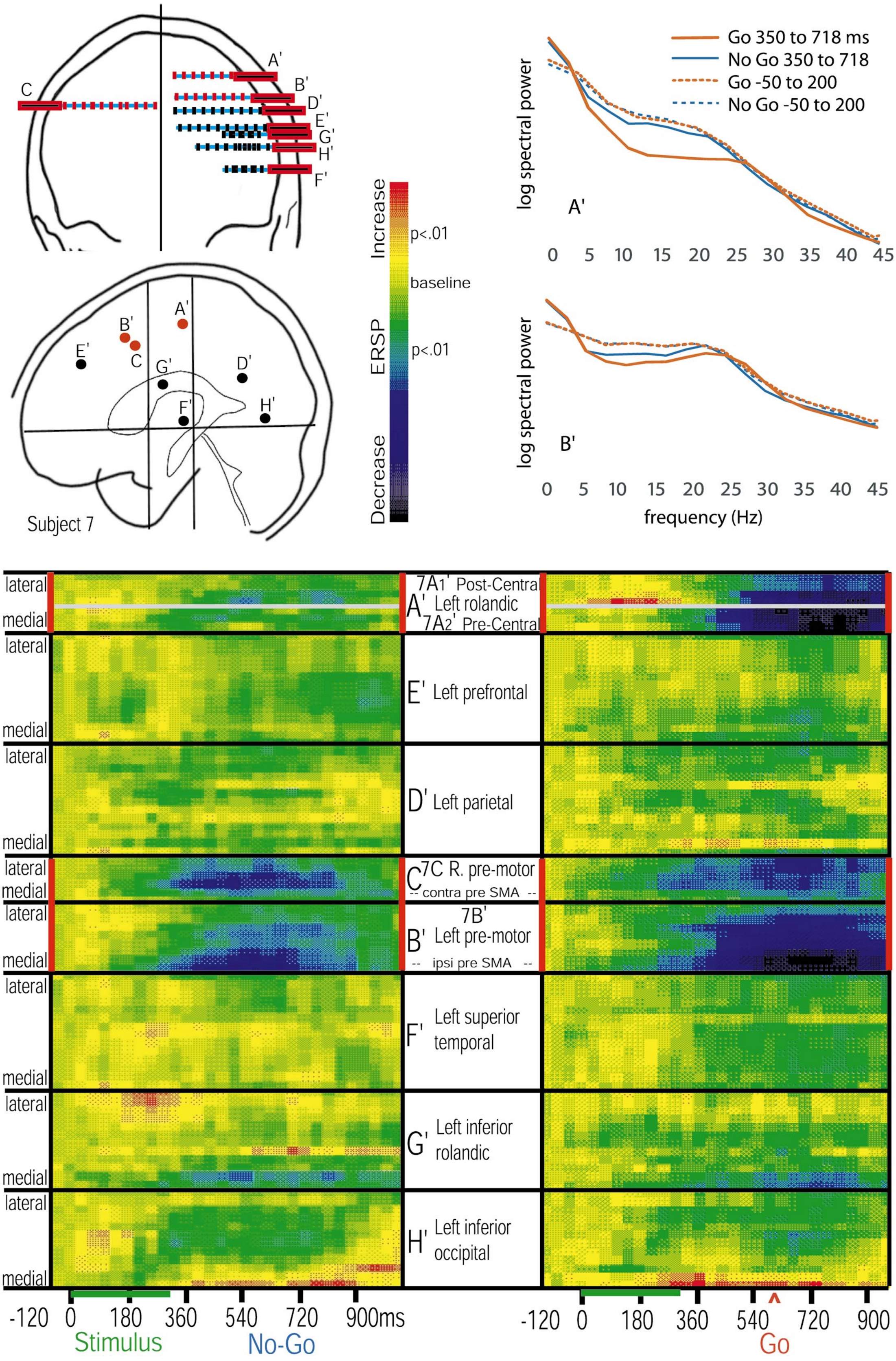

FIG. 3. Statistical parametric *z* score maps based on peri-Rolandic iEEG event-related spectra are shown below. Upper left: Brain schemas illustrating the saggital and coronal locations of all iEEG depth electrode probes for subject 7. Upper right: Spectral power at all frequencies are plotted for GO *versus* NO-GO trials (red vs blue lines) of the DR task, at peri-stimulus vs peri-response latencies (dashed vs solid lines). Note the broadband decrease in spectral power associated with the movement, in both the rolandic fissure (A′) and the

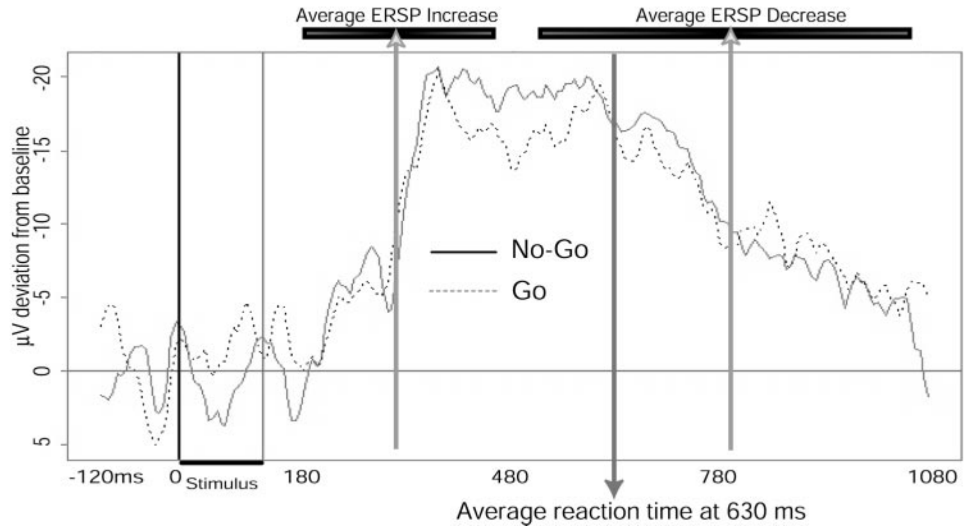

FIG. 4. Peri-Rolandic across-subject average of iEEG event related potentials in GO versus NO-GO trials. Across subject ERP averages were computed from two electrode contacts from each subject recorded during the DR task (Table 1). Electrode contacts were chosen on the basis of those showing the greatest ERSP decrease during movement. Upward pointing arrows indicate the center of the average iERSP increase and late decrease. The average response time is indicated by the center, downward pointing arrow. Little or no difference is apparent between go and no-go trials.

normalized iERSP values shows a clear movement-associated iERSP decrease with an onset around 350 ms. Given the shorter recording epochs that were obtained during the lateralized visual discrimination task, the iERSP decrease generally continued past the movement and to the end of the recording. Thus, an average duration of the iERSP decrease could not be accurately estimated. The iERSP decrease generally appeared across a wide frequency range (8–45 Hz) and is most prevalent in the beta^1 and beta^2 frequency bands (13–22 Hz). The aERSP, as in the DR task, did not reveal any movement-related change in spectral power, because it is insensitive to decreases in spectral power. The iERSP of the LVD task did not show an early iERSP increase as had been seen in the DR task. However, the aERSP appears to show a bilateral, movement-related aERSP increase from ~225–300 ms.

The 18–22 Hz LVD iERSP time course for peri-Rolandic cortex is illustrated for a representative individual (subject 9) in Fig. 7. The movement condition (right half of figure) shows a distinct iERSP decrease during the button press phase of the task. In contrast, the nonmovement condition (left half of figure) lacks this feature. As seen in the DR task, movement-associated iERSP decreases occur bilaterally to the hand movement. Movement associated iERSP decreases are preceded by a weak and variable iERSP increase in this subject. Across all subjects, early iERSP increases did not occur as reliably in the LVD as in the DR task (Fig. 6 versus Fig. 5).

Event related potentials were averaged across electrode contacts from all subjects that performed the LVD task. As in the DR task, an event-related readiness potential is apparent in the go-condition (Fig. 8). However, in the DR task this readiness potential also occurs with the no-go trials (i.e., regardless of the movement condition). Thus, unlike the DR task, the multisubject average ERP from the LVD task did yield a clear distinction between movement and nonmovement responses. In both ipsilateral and contralateral hand movement conditions a negative potential begins at around 400 ms that does not occur in the nonmovement condition (Fig. 8).

Precentral versus Postcentral

No consistent differences were seen in the pre- versus postcentral ERSP measures. In order to reduce the possibility that volume-conducted activity generated precentrally would be recorded postcentrally (or vice versa), we used next-neighbor electrode contact bipolar derivations to calculate ERP and ERSP. These were

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supplementary motor cortex (B′). Bottom: The temporal evolution of this decrease is shown with maps of iERSP from 13–24 Hz during movement (GO; right) and nonmovement (NO-GO; left) conditions. The iERSP maps organize iEEG contacts from medial, at the bottom of the map, to lateral, toward the top, for each depth probe. Widespread iERSP decreases are seen in both conditions but are stronger in the movement condition. This subject shows an early iERSP increase preceding the iERSP decrease with focal specificity in the left postcentral Rolandic region for the movement condition (ipsilateral to hand movement). However, such occurrences are not regularly seen across patients and the early iERSP increase is usually of similar amplitude between movement and nonmovement conditions.

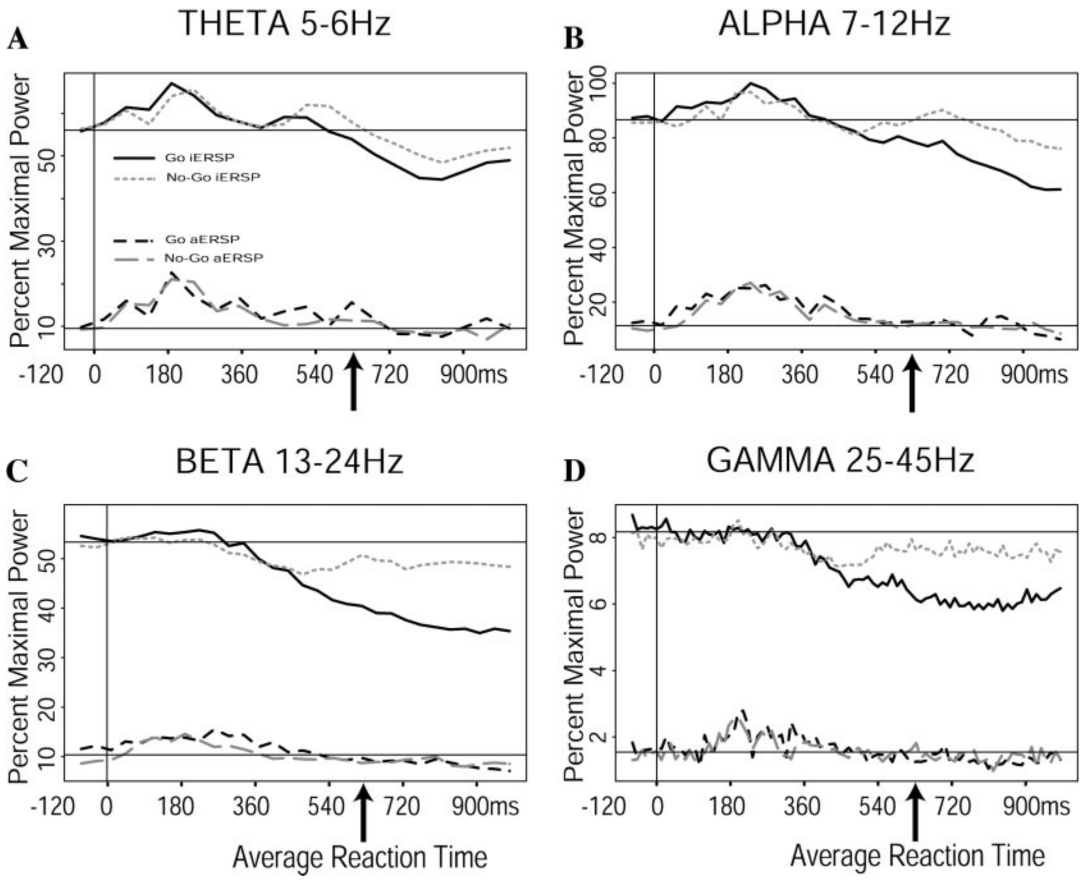

FIG. 5. Peri-Rolandic across-subject average of iERSP & aERSP for the DR task in GO versus NO-GO trials. The across subject iERSP and aERSP averages were computed from the same set of electrode contacts as described in the legend of Fig. 4 (Table 1). Frequency bands are displayed for 5–6 (A), 7–12 (B), 13–24 (C), and 25–45 (D) Hz. iERSP timecourses reveal the early movement nonspecific increase that are most prevalent in the low frequency range (5–12 Hz). Late iERSP decreases are seen in the full range of frequencies (5–45 Hz) and are most movement selective in the upper frequencies (7–45 Hz).

calculated for electrodes with contacts in both pre- and postcentral cortex. No obvious differences were seen in either the iERSP or aERSP of these anatomically distinct, but adjacent regions (Fig. 9, for an individual example). Similarly, iERSP decreases are present in both superior and inferior Rolandic sites (e.g., Fig. 2). Of particular interest is the observation that both sides of the Rolandic fissure show a late movement-related iERSP decrease across a wide frequency range with no statistically significant differences. Statistical power calculations, using an alpha value of 0.05, based on the four subjects with pre- and postcentral recordings predicted a 0.004% chance that significant differences between pre- and postcentral regions in the late ERSP decrease were overlooked. While no clear inversion examples were found in the data set, local generation is supported by commonly observed amplitude gradients between adjacent contacts (Fig. 10). While individuals showed a wide variability, other areas, including premotor, cingulate, and supplemental motor areas, revealed no consistent differences in the direction or latency of ERSP time courses.

DISCUSSION

Early EEG studies suggested that high amplitude rhythmic activity is inversely related to mentation. For example, the alpha rhythm appears when the eyes are closed (Berger, 1929), and delta activity occurs during nondreaming sleep (Loomis *et al.*, 1936). This observation agrees with the generally held view of Rolandic mu rhythms as reflecting a resting or idle state. In this study we show broad band movement related decreases in the spectral power of peri-Rolandic iEEG. This also fits with the interpretation of Rolandic mu rhythms as a resting/idle state where decreases in the organization and amplitude of this rhythm are taken as a sign of activation. In contrast, previous investigations using analytic techniques similar to those presented here but in the fusiform cortex have associated increases in spectral power with active processing of faces (Klopp *et al.*, 1999). This is a region known to make a specific contribution in face processing at the moment of spectral power increase (Damasio *et al.*, 1990; Halgren *et al.*, 1994a). Therefore, it appears that alterations in

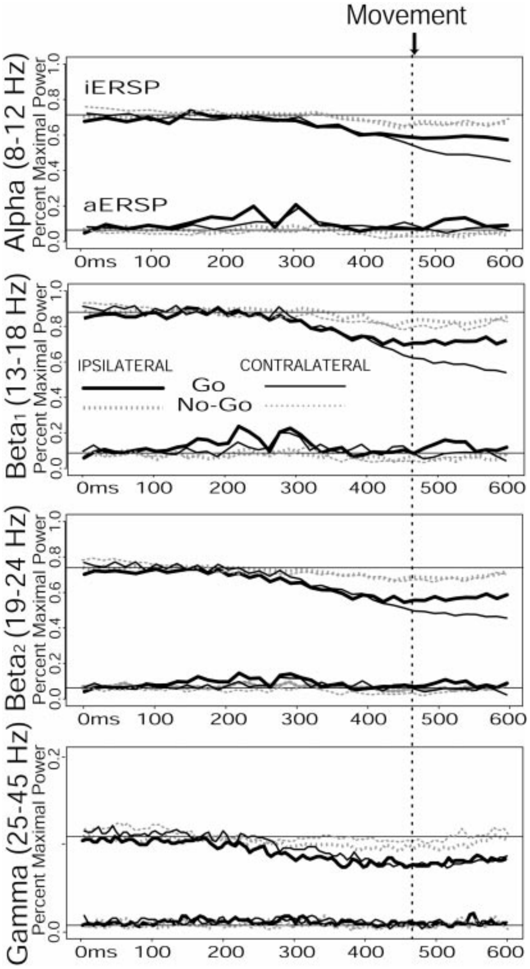

FIG. 6. Peri-Rolandic across-subject average of iERSP & aERSP for the LVD task. The across subject iERSP and aERSP averages were computed from two representative electrode contacts from each region and each subject (Table 2) and show ipsilateral and contralateral response hands (heavy and light lines) combined with target (Go) and nontarget (No-Go) conditions (continuous and dotted lines). Frequency bands include alpha (8–12 Hz), beta1 (13–18 Hz), beta2 (19–24 Hz), and gamma (25–45 Hz). Power is given in percentage of the maximal values (which occurred in the beta1 band). Late iERSP decreases are present in all bands, and are selective for the movement condition. Additionally, they occur to a greater degree contralateral to hand movement. For example, the contralateral iERSP decrease from baseline in the beta1 frequency range is as much as twice as large than the ipsilateral iERSP decrease. Average response latency is denoted by the vertical dotted line.

spectral power may reflect either activation or inactivation depending on the brain region and time relative to stimulus.

While the Rolandic mu rhythm is found with scalp EEG in only a minority of subjects, it has been suggested that all healthy adults produce it (Niedermeyer, 1997). This claim is supported by the fact that each of our subjects produced clear movement-related attenuation of power within the frequency range of mu rhythms. Previous investigations of Rolandic mu rhythms generally employ self-paced, predetermined movements (Pfurtscheller and Neuper, 1992; Derambure *et al.*, 1997; Leocani *et al.*, 1997). In contrast, both the DR and the LVD tasks require the subjects to make prompt stimulus dependent go/no-go motor decisions. It is thus conceivable that the early transient iERSP increase seen here in the DR task that occurred immediately after stimulus presentation and prior to movement represents motor programming, and that its absence in previous scalp EEG studies is due to that programming being essentially complete prior to the task. However, it seems more likely that this iERSP increase may reflect an early inhibitory state that prevents motor cortex involvement during the earliest stages of stimulus processing.

Similar early iERSP increases were not consistently found in the LVD task. Nevertheless, one should note that individual cases do show this increase (Fig. 7). Given the fact that the LVD task was less cognitively demanding (respond to a single simple target stimulus) compared to the DR task (respond to face or word if it belongs to a set of repeating stimuli), it is possible that the LVD task required less pre-movement inhibition. Alternatively, since the visual processing required by the DR task was more complex, the early increase in Rolandic spectral power could represent a time when the motor areas are “less in use” during intense visual processing, as opposed to being “actively inhibited.”

A large ERP change occurs in Rolandic cortex from 360 to 600 ms in both tasks. This measure fails to reveal any difference between movement conditions in the DR task. In contrast, the iERSP measure on the same data set consistently showed a robust movement-specific decrease. This contrast clearly implies that the neuroelectric activity that gives rise to the movement-specificity is not phase-locked to the stimulus. The baseline of aERSP will tend toward zero given that the phase before stimulus onset is typically random. Therefore, it should not be possible to observe significant decreases relative to the baseline in the aERSP, and this measure revealed no movement-specificity in the mu decrease. A similar inability of aERSP to measure decreases in spectral power was noted in an earlier study of the fusiform gyrus response to faces (Klopp *et al.*, 1999). These observations emphasize that, although computationally costly, individual trial data must be analyzed to arrive at a complete view of event-related spectral changes.

iERSP analysis of the DR task suggests a gradual accumulation of information in Rolandic cortex prior to movement. Both go and no-go conditions elicit an iERSP decrease starting around 250 ms, and continuing until around 450 ms when the two conditions diverge. Transcranial magnetic stimulation studies suggest that the conduction velocity from motor cortex are in the range of 50–70 meters/second (Fujiki *et al.*, 1996). Given that the iERSP decrease began ~200 ms

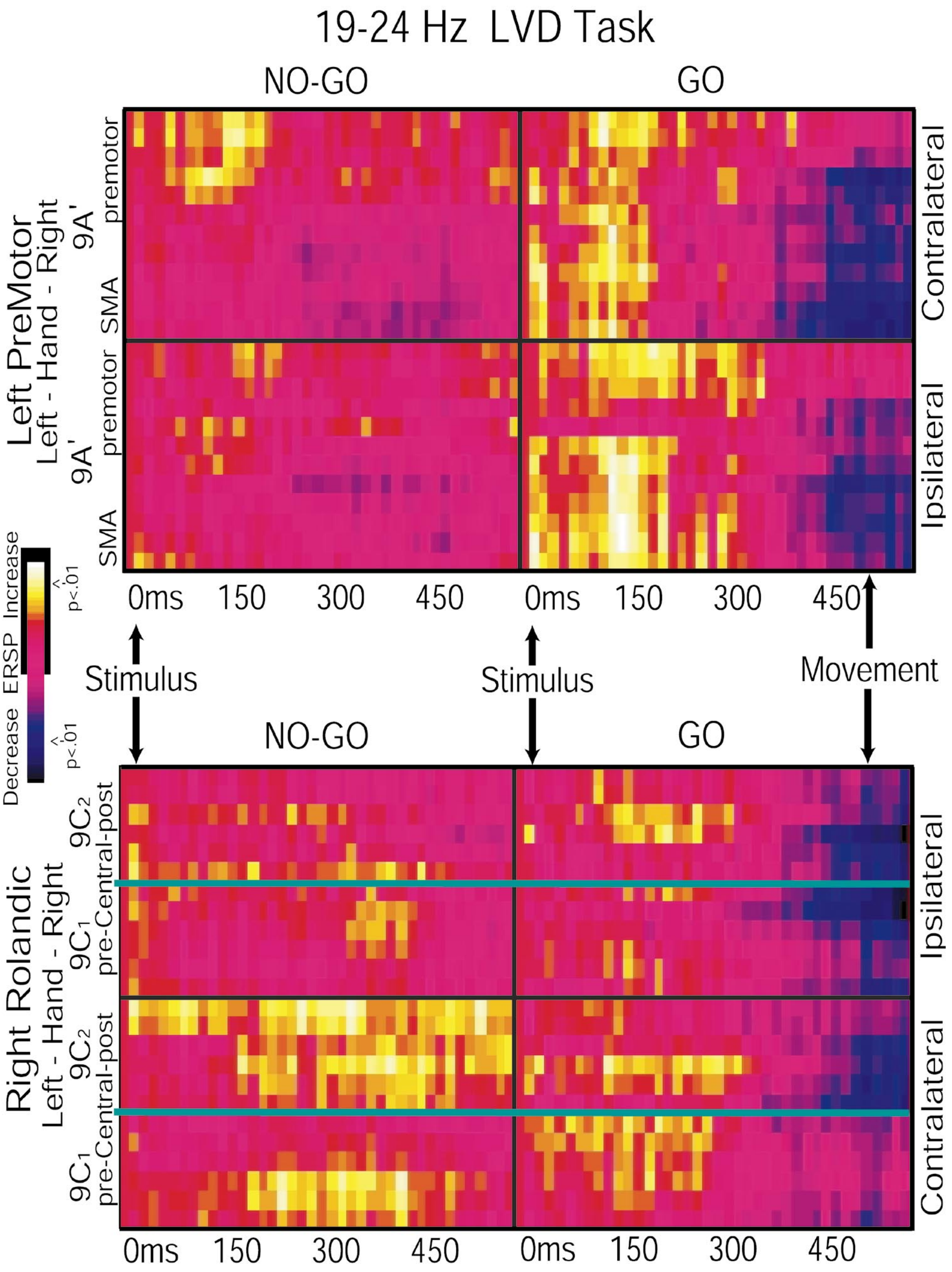

FIG. 7. Statistical parametric *z* score maps based on peri-Rolandic iEEG event-related Beta^2 (19–24 Hz) spectra of the LVD task. iERSP maps from electrodes 9A′ (top) and 9C$_1$ & 9C$_2$ (bottom) are shown for each of the four conditions. The iERSP maps organize iEEG contacts from medial at the bottom of the map and lateral towards the top for each depth probe. Precentral and postcentral contacts are separated by a thin green line in the bottom four iERSP maps. Late widespread iERSP decreases are apparent bilaterally in the movement condition. Although this subject appears to show some early bilateral iERSP increases, especially in probe 9A′ for the movement condition, the LVD task did not reliably produce this effect across subjects. It should be noted that while the iERSP decrease appears to be greater in the ipsilateral Rolandic recording (9C$_2$), only the iERSP decrease relative to baseline is statistically significant.

prior to the average reaction time, it appears that this spectral decrease commenced well before command generation in motor cortex. Selection of a movement plan may continue the ERSP decrease in the go condition. In contrast, selection of a no-movement plan may abort an extended ERSP decrease. This argues against a serial-processing model of movement decision/planning.

A different pattern, with similar implications was seen in the LVD task. Unlike the DR task, which requires more extensive recognition processing of words, the LVD task is a motor response to a simple

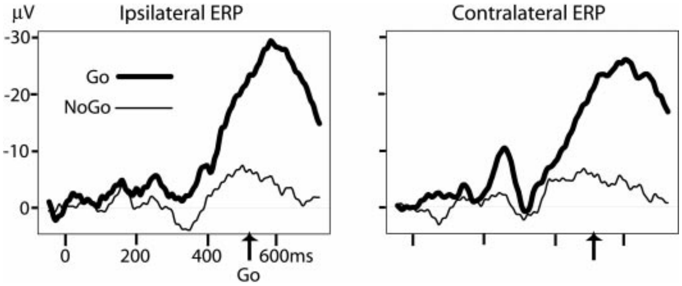

FIG. 8. Peri-Rolandic across-subject average of intracranial event related potentials for the LVD task. Across-subject ERPs were computed from 2 representative electrode contacts from each region and each subject (Table 2). Separate waveforms are shown for target (Go) and nontarget (No-Go) conditions, for responses by the ipsilateral (left column) and contralateral (right column) hands. These ERPs show movement-selective late bilateral negative components which peak at around 560 ms, as well as a smaller negative component at 250 ms that is contralateral to the movement.

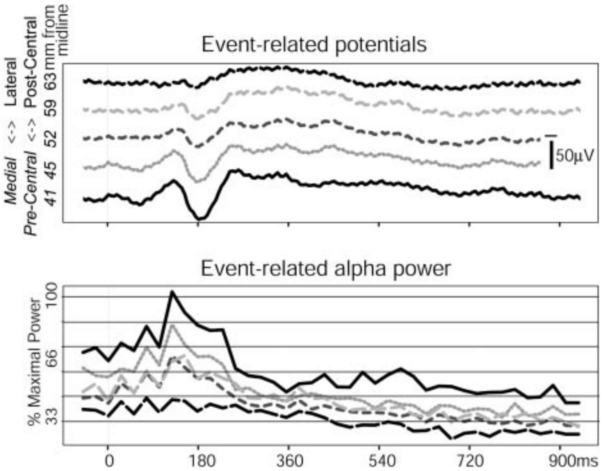

FIG. 10. Amplitude gradients and alpha power distribution in precentral vs postcentral cortex. ERPs and iERSP are shown for the movement condition in the DR task for 5 adjacent contacts in subject 2. The electrode passes from postcentral cortex (lateral 2 contacts) to precentral cortex (medial 3 contacts). A smooth transition is observed with larger ERP amplitudes in precentral cortex. Spectral power fluctuation in the alpha frequency range (8–12 Hz) shows an early increase that is strongest in precentral cortex but occurs to a lesser extent in the postcentral electrode contacts. All electrode contacts show a subsequent decrease in iERSP relative to baseline values.

target symbol. Furthermore, the frequency of targets differs between the tasks. While the DR task is composed of 50% target stimuli, the LVD task contains only 12.5% targets for each hand. The strategy in the DR task may be to prepare to move on each trial, and to cancel that expectation when the stimulus is identified as a nontarget. In contrast, the strategy in the LVD task may be to start movement preparation (for both hands) only when the stimulus is identified as a target, and then focus the preparation to the contralateral Rolandic area as the response is progressively defined. Thus, in the LVD task, the Rolandic iERSP begins to distinguish go from no-go trials at ~250 ms after stimulus onset, and then contralateral from ipsilateral movement at ~400 ms. In this case the ERP does distinguish go from no-go trials, but not contralateral from ipsilateral movements, again demonstrating the utility of this measure. Combining the iERSP results from both tasks, it is clear that the mu desynchronization begins long before the actual movement, and demonstrates a progressive specificity as the movement approaches.

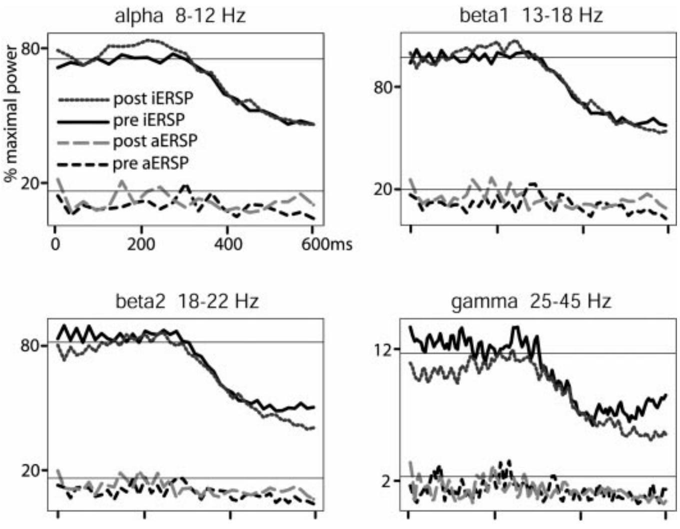

FIG. 9. Next-neighbor bipolar derivations of iERSP & aERSP for pre- and postcentral gyrus. Bipolar derivations for pre- and postcentral gyrus iERSP and aERSP time courses are shown for subject 9. A decrease in spectral power is seen in all frequency bands beginning at about 300 ms. Power is given in percentage of the maximal values (which occurred in the beta^1 band). No clear differences are seen between pre- and postcentral gyrus recordings.

The event-related potentials recorded in the LVD task generally do not show ERP components that can be lateralized to the response hand. There is an exception of an early component centered at 250 ms that appears to be lateralized to the hemisphere contralateral to movement (Fig. 8). This is largely from the contribution of a single subject (subject 9). Of the six subjects performing the LVD task only one (subject 9) produced significant lateralized ERP components in some of the depth EEG contacts (see (Clarke *et al.*, 1999) for examples of individual ERPs). Previous scalp motor studies have shown lateralized motor potentials, presumably generated by the primary Rolandic motor area, MI (Deecke, 1990). However, readiness magnetic fields have been reported prior to a variety of voluntary movements that display a topography indicative of bilateral source activation even when instructions demand unilateral movement (Weinberg *et al.*, 1990). Variability in the movement-evoked field across individuals, which are more evident in MEG than in EEG, may reflect the summation of multiple sources active in the region of the sensorimotor cortex during movement onset (i.e., both pre- and postcentral generators as well as premotor, cingulate, and supplementary motor areas).

Event related desynchronization studies also show lateralized changes in the mu rhythm (Pfurtscheller and Neuper, 1997). Hand dominance and type of movement appear to influence the proportion of premovement mu-rhythm desynchronization in the left and right peri-Rolandic area (Stancak and Pfurtscheller, 1996). The findings based on the LVD task presented here also show a lateralization of iERSP decrease to the hemisphere contralateral to hand movement (it was not usually possible to compare the ipsilateral and contralateral responses in the DR task, where contralateral recordings were rare). While both hemispheres show a late decrease in iERSP, contralateral decreases within the mu frequency range were as much as twice the amplitude of ipsilateral decreases (Fig. 6).

Neuromagnetic (Salmelin and Hari, 1994b; Salmelin *et al.*, 1995) recordings have attempted to distinguish between two separate mu rhythms with different functional roles. A 10 Hz rhythm was modeled as originating predominantly in the primary somatosensory cortex and hypothesized to be a true somatosensory rhythm. In contrast, a reported 20 Hz rhythm was modeled as originating from the anterior bank of the central sulcus and was hypothesized to be essentially somatomotor. These claims were based on equivalent current dipole modeling of extracted single dipoles using time-varying multidipole analysis to verify the alternating dominance of individual sources. No reliable distinction between pre- and postcentral mu rhythms could be made based on intracranial data in this study. Our data suggest that the signal source of the late iERSP decrease extends throughout pre- and postcentral cortex as well as cingulate and premotor. In all regions, the task-related changes had similar time courses and were approximately equally prominent across the entire sampled frequency spectrum (from 5 to 45 Hz), rather than being confined to narrow frequency bands close to 10 and 20 Hz. Broadband spectral power decreases of the Rolandic mu rhythm were seen in another intracranial study using EEG electrode grids on the surface of the cortex (Arroyo *et al.,* 1993). However, this discrepancy may only be apparent, inasmuch as the distinctions between 10 and 20 Hz rhythms were clearest in the hand area during the postmovement period, whereas the current recordings were mainly outside the hand area, during the premovement period.

Overall the current findings suggest that the peri-Rolandic region is activated well before the production of a final movement command. Studies on nonhuman primates show gamma-band oscillations in local field potentials and single unit discharge activity that are most prominent during a premovement delay period. These oscillations decrease with the appearance of the firing rate modulation coupled to the motor action, i.e., immediately before the actual movement (Donoghue *et al.*, 1998). Furthermore, cross-correlation analysis revealed that local field potential oscillations were synchronous over long distances (>7 mm) across primary motor and premotor cortex (Sanes and Donoghue, 1993). This transient and early mu oscillation increase before movement onset was also seen here in the DR task (Fig. 2).

The premotor, SMA, pre-SMA, and dorsal cingulate are additional regions that have all been shown to be vital in the preparation for and the guidance of movements (Wise, 1985; Picard and Strick, 1997). Motor unit activity in premotor and supplementary motor areas both show separate populations of cells active during the premovement versus the movement period (Romo and Schultz, 1987; Mushiake *et al.*, 1991). While these distributions vary depending on the conditions of the task (i.e., if instructions are internally versus externally generated), they clearly show that premovement activity is widespread and may relate to the wide distribution seen in the iERSP decrease.

In summary, these data show that the iERSP measure produces stable patterns that are specific to the task, brain region and timing relative to stimulus presentation and movement. We suggest that the early iERSP increase could reflect either functional inhibition or movement preparation, whereas the late peri-Rolandic iERSP decrease represents a state of transient functional activation. The late iERSP decrease appears to be a widespread phenomena that occurs prior to and during movement and across a broad frequency range. Whereas the early increase is seen in both individual trial (iERSP) and averaged (aERSP) data, the late decrease is seen only in the iERSP. These data clearly support the contention of a gradual buildup of information in motor-related cortex prior to motor decision. Moreover, it appears this process is highly distributed inasmuch as ERSP decreases occurred in both pre- and postcentral as well as cingulate and premotor cortices.

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