

Event-Related Changes in Neuromagnetic Activity Associated With Syncopation and Synchronization Timing Tasks

Justine M. Mayville,¹ Armin Fuchs,^{1*} Mingzhou Ding,¹ Douglas Cheyne,²
Lüder Deecke,³ and J.A. Scott Kelso¹

¹Center for Complex Systems and Brain Sciences, Florida Atlantic University, Boca Raton, Florida

²Simon Fraser University, Vancouver, BC, Canada

³Department of Clinical Neurology, University of Vienna and General Hospital, Vienna, Austria

Abstract: For low rhythmic rates (1.0 to ~2.0 Hz), subjects are able to successfully coordinate finger flexion with an external metronome in either a syncopated (between the beats) or synchronized (on each beat) fashion. Beyond this rate, however, syncopation becomes unstable and subjects spontaneously switch to synchronization to maintain a 1:1 stimulus/response relationship. We used a whole-head magnetometer to investigate the spatiotemporal dynamics of neuromagnetic activity (MEG) associated with both coordinative patterns at eight different rates spanning the range 1.0–2.75 Hz. Timing changes in the event-related fields accompanied transitions from syncopation to synchronization and followed the placement of the motor response within each stimulus/response cycle. Decomposition of event-related fields into component auditory and motor brain responses revealed that the amplitude of the former decreased with increasing coordination rate whereas the motor contribution remained approximately constant across all rates. Such an interaction may contribute to changes in auditory-motor integration that cause syncopation to become unstable. Examination of event-related changes in high frequency bands revealed that MEG signal power in the beta band (15–30 Hz) was significantly lower during syncopated coordination in sensors covering the contralateral sensorimotor area suggesting a dependence of beta rhythm amplitude on task difficulty. Suppression of beta rhythms was also stronger during synchronization preceded by syncopation, e.g., after subjects had switched, when compared with a control condition in which subjects synchronized throughout the entire range of rates. *Hum. Brain Mapping* 14: 65–80, 2001. © 2001 Wiley-Liss, Inc.

Key words: MEG; sensorimotor coordination; phase transition; auditory; motor; beta rhythm

INTRODUCTION

When people are directed to coordinate unimanual finger flexion with an external metronome in a 1:1 fashion, their ability to do this depends on when they time their movement within the metronome cycle. A synchronized (on-the-beat) mode of coordination is typically established very rapidly (one to two cycles) if the range of metronome frequencies is within what one would normally call rhythmic, ~0.6–4.0 Hz [Frasse, 1982]. Below this range, anticipation of the metronome is difficult whereas for faster rates, there

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*Correspondence to: Armin Fuchs, Center for Complex Systems and Brain Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, FL, 33431. E-mail: afuchs@fau.edu

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exist both perceptual and biomechanical limitations. Off-the-beat timing relations, however, are much more difficult and can typically only be performed for lower rhythmic rates (<2.0 Hz). An interesting consequence of this fact is that if people are asked to syncopate with a metronome (i.e., move between consecutive beats), and the rate of the metronome is then systematically increased, a spontaneous transition to synchronization occurs at a critical metronome frequency [Kelso et al., 1990]. Two key dynamical features precede this transition. First is an increase in the variability of the phase relationship between the subject's response and metronome onset (180° would be perfect syncopation). The second is an increase in the amount of time it takes for subjects to recover a syncopated pattern in response to external perturbations (e.g., via a torque motor), also known as critical slowing down. Both of these signatures of instability are hallmark features of self-organization in nonlinear dynamical systems. [see Haken, 1996; Kelso, 1995 for reviews].

The reason why syncopation becomes unstable is not known. It may be due to the fact that synchronized patterns are learned from childhood whereas 'between beats' timing patterns are less common. It is clearly not a biomechanical problem resulting from faster movement rates, however, because synchronization remains possible. Likewise, subjects are perfectly able to perceive distinct metronome events in this frequency range. Therefore, the answer must somehow lie in the way the perception of the metronome is coupled to the motor response. Given that this coupling occurs centrally, an obvious question is whether differences between syncopated and synchronized coordination translate into differences in the spatiotemporal dynamics of brain activity.

Research conducted over the last 10 years using both EEG and MEG demonstrates that there are several observable changes in patterns of neural activity that accompany a transition from flexion off-the-beat to flexion on-the-beat induced by increases in the rate of a pacing auditory metronome. The earliest studies to address this issue employed a 37-SQUID (Superconducting Quantum Interference Device) system centered over the contralateral hemisphere [Fuchs et al., 1992; Kelso et al., 1991, 1992]. Results showed a topographic reorganization of the dominant pattern of magnetic field activity coincident with the shift in timing on the behavioral level. In addition, there was a parallel 180° shift in the phase of the event-related field relative to the rate of coordination. Unfortunately, the limited sensor coverage made physiological interpretation difficult by precluding knowledge as

to whether these effects were observable over other regions of the head. Furthermore, the lack of a transition-free condition made it impossible to determine whether these topographic effects were due to the change in coordinative timing or simply the increase in coordination rate.

Later work addressed these limitations by using a whole-scalp 61-channel EEG recording system that provided homogeneous coverage over the entire scalp surface. Differences in event-related potential signal power and phase at the coordination frequency were found to uniquely relate to the mode (syncopate vs. synchronize) rather than the rate of coordination [Mayville et al., 1999; Wallenstein et al., 1995]. These differences were confined to electrodes located over contralateral central and centro-parietal recording sites suggesting a change in the dynamics of activity in the underlying sensorimotor cortex (SM1) though effects of volume conduction inherent to EEG technology made it problematic to segregate auditory from motor-related brain activity.

Our aim here is to develop a physiological interpretation of spatiotemporal changes in brain activity that occur when subjects transition from syncopated to synchronized coordination. Through the use of a 143-SQUID whole head system we gain not only the advantage that MEG signals are not subject to smearing or volume conduction but also a tremendous increase in sensor coverage. Together these advantages afford the spatial resolution necessary to separate auditory and motor-related neural events. We examine differences in neuromagnetic activity associated with a condition in which subjects transitioned from syncopation to synchronization as well as a second transition-free condition in which subjects synchronized throughout the same range of frequencies. The second condition serves as a control for the served effect of frequency.

We further extend our analyses to include an investigation of high frequency oscillations, which though event-related, are not necessarily phase-locked to any task event and thus often average out if ensemble averaging is done in the time domain. Several brain rhythms are known to exhibit movement-related changes in amplitude. For example, both the mu (8–12 Hz) and beta (15–30 Hz) rhythms show a decrease in power before movement over contralateral sensorimotor and midline premotor areas as well as during movement bilaterally. This phenomenon is referred to as event-related desynchronization (ERD) [Pfurtscheller, 1981; Pfurtscheller and Aranibar, 1977]. ERD is thought to reflect a shift from 'idling' to task-related activity in underlying thalamocortical and corticocortical networks [Pfurtscheller and Lopes da

Silva, 1999], an interpretation supported by the fact that both rhythms 'resynchronize' after termination of movement. [Salmelin and Hari, 1994; Pfurtscheller et al., 1996].

The majority of studies on motor-related changes in non-phase locked rhythms have examined self-paced, discrete finger movements. The dependence of such amplitude changes on movement parameters such as rate or task complexity is not well understood. Recent work by Manganotti et al. [1998] indicates that suppression of high frequency brain rhythms is stronger for more complex movement tasks, especially for rhythms in the mu frequency range. In contrast, Nashmi et al. [1994] found that drawing tasks resulted in significant increases in gamma (30–50 Hz) activity if subjects were instructed to focus on accuracy of the movement trajectory. Both effects were stronger over contralateral sensorimotor areas and have been attributed to the degree of motor planning or attention necessary to perform more difficult task conditions. A correlation between high frequency oscillations and attention has also been observed in animal recordings [Lopes da Silva, 1991; Lopes da Silva et al., 1970; MacKay, 1997; Murthy and Fetz, 1992].

Here we ask whether the strength of rhythms in the mu (8–12 Hz), beta (15–30 Hz) and gamma (30–50 Hz) ranges has any dependence on whether subjects are coordinating in a syncopated versus a synchronized manner. Given the inability of subjects to syncopate at higher rates, it is reasonable to conclude that off-the-beat relations are more difficult in general, requiring greater attentional focus. This conclusion is supported by recent behavioral work showing that anti-phase coordination in a bimanual task (analogous to syncopation in a unimanual situation) is associated with slower responses in a simultaneous probe reaction time task as compared with in-phase (synchronized) movements [Temprado et al., 1999; see also Carson et al., 1999]. Of particular interest is whether differences in the amplitude of these rhythms are observable over contralateral sensorimotor areas because the prior EEG and MEG studies conducted by our group indicate large-scale reorganization of neuronal activity in this region when subjects switch from syncopation to synchronization.

METHODS

Subjects

This experiment was in compliance with all standards of human research outlined in the Declaration of Helsinki as well as by the Institutional Review

Board. Four subjects (three males, one female) whose ages ranged from 27–41 participated. All subjects reported being right-handed. Informed consent was obtained from all subjects before any MEG recording. Data from three subjects is reported here; the MEG signals from one of the male subjects were corrupted because of dental fillings.

Task conditions

The experiment consisted of two auditory-motor coordination conditions and two control conditions. In the coordination conditions, subjects listened to an auditory metronome (1 kHz, 60 msec tones) and were instructed to time *peak* flexion of their right index finger either exactly between consecutive beats (Syncopate condition) or on each beat (Synchronize condition). The rate of the metronome was systematically increased on each trial from 1.0 Hz to 2.75 Hz in 0.25 Hz increments every ten cycles. Each set of 10 cycles at a constant rate is referred to as a *plateau*. Subjects were further told to maintain a 1:1 stimulus/response ratio throughout the entire trial and not to intervene even if they felt their timing pattern begin to change. These rates (1.0–2.75 Hz) were chosen because it is known that subjects are unable to maintain a syncopated mode of unimanual sensory-motor coordination across this range [Kelso et al., 1990, 1992]. Each subject performed 16 trials of both coordination conditions, yielding a total of 160 cycles per plateau frequency.

In the first control condition (Auditory condition), subjects listened to tones (approximately 80) presented with randomized intervals of 2–4 sec. In the second control condition (Motor condition), subjects were asked to self-pace flexion movements with inter-response intervals of 2–4 sec; around 60–80 responses were collected for each subject. These controls were included so that brain responses to the component events in the coordination tasks could be identified for each subject.

Experimental procedure

Experiments were carried out at the Department of Clinical Neurology at the University of Vienna. Subjects participated in all conditions while seated inside a magnetically shielded room (Vacuum Schmelze, Hanau) and with their heads held firm within the dewar helmet. The metronome was delivered binaurally through plastic headphones at a volume that the subjects reported to be comfortable. Subjects responded with almost-isometric right index finger flexions against a sensitive air cushion that was connected

to a pressure-voltage transducer located just outside the room. Due to the length of tubing that connected the cushion to the transducer (10 m) response signals were corrected off-line for a delay of 33 msec that is the time it took for pressure changes to arrive at the transducer (given by the length of tubing divided by the speed of sound in air). Subjects were asked to fixate at a point located approximately 2 m in front of them and to confine all eye or extraneous body movements to breaks between trials.

Data acquisition

MEG activity during all four conditions was recorded using a whole-head magnetoencephalograph (CTF Inc., Port Coquitlam, Canada) comprised of 143 SQUID sensors distributed homogeneously across the scalp. Conversion to third-order gradiometers was performed in firmware using a set of reference coils. MEG, metronome and response signals were band-pass (0.3–80 Hz) and notch filtered (50 and 100 Hz). Digitization was done at a rate of 312.5 Hz. A coordinate system for each subject's head was defined with respect to three fiduciary points: the nasion, left, and right preauricular points (whose three-dimensional coordinates were measured before each experiment using a set of reference coils). Finally, sensor coordinates were projected into two dimensions for topographical mapping.

Behavioral analysis

Metronome and response signals from the coordination conditions were used to determine the timing relationship employed by subjects on a cycle-by-cycle basis. One cycle was defined as one period of the metronome, i.e., $\frac{1}{2}$ period before tone onset to $\frac{1}{2}$ period after. First, two points in each cycle were marked: the onset of the metronome tone and the peak of the response (corresponding to point of maximal flexion). Second, the relative phase between these two points was calculated. Finally, these phase values were subjected to criteria that segregated each cycle into one of three categories: 1) syncopated coordination ($180^\circ \pm 60^\circ$), 2) synchronized coordination ($0^\circ \pm 60^\circ$), or 3) other. Cycles classified as 'other' were excluded from further analysis.

MEG analysis: control conditions

The purpose of these conditions was to obtain the primary field pattern evoked by either an auditory tone or flexion event for each individual subject. All

MEG data were manually inspected for eye blinks or other artifacts. Contaminated segments were marked and discarded from averaging procedures. Ensemble averaging (i.e., across trials) was done separately for each subject using a one-second window centered at tone onset for the Auditory condition and at peak flexion for the Motor condition. The principal field patterns were obtained by applying the Karhunen-Loève decomposition technique (also known as Principal Components analysis) to the ensemble average and taking the top eigenvector, i.e., the spatial pattern that accounted for most of the signal variance. Topographic mapping of field patterns was done by projecting three-dimensional sensor coordinates into two-dimensional space and then interpolating between sensor positions with a spline of 3rd order.

MEG analysis: coordination conditions

MEG signals were again manually inspected for artifacts. If any portion of a cycle was contaminated, the entire cycle was discarded from further analysis. Remaining cycles were then separated into groups according to subject, coordination condition, plateau frequency (i.e., metronome rate) and timing mode within plateau (syncopation or synchronization). Ensemble averages were computed separately for each group of cycles resulting in event-related fields. Timing differences in event-related field components were investigated by applying a discrete Fourier transform and plotting the phase of the fundamental frequency in the resulting spectra. Because each event-related field was one cycle (metronome period) in length, the fundamental frequency in Fourier space always corresponded to the coordination or plateau frequency in the experiment. Amplitude changes were examined by plotting total spectral power. To assess the contribution of auditory and motor-related patterns brain activity associated with syncopation or synchronization, patterns obtained from the control conditions performed by each subject were projected onto event-related fields from the coordination conditions using a dual-basis projection technique [Friedrich and Uhl, 1996; Fuchs et al., 2000b].

MEG data from the coordination conditions were also analyzed without ensemble averaging in the time domain to investigate whether task-related effects are observable for higher frequency bands (e.g., alpha, beta) that are not necessarily phase locked cycle to cycle. The raw cycles in each data group were first preprocessed by subtracting the corresponding event-related field to meet stationarity requirements for spectral estimation [see Bendat and Piersol, 1986 for

TABLE I. Average relative phase ($\pm$ SD) between peak response and tone onset*

	1.0 Hz	1.25 Hz	1.5 Hz	1.75 Hz	2.0 Hz	2.25 Hz	2.5 Hz	2.75 Hz
Syncopate condition								
S1	143.2 (19.3)	153.7 (17.1)	164.0 (18.4)	189.7 (21.9)	25.6 (24.6)	34.2 (13.9)	34.0 (14.6)	24.5 (20.8)
S2	152.5 (27.8)	161.7 (33.5)	164.8 (30.0)	184.1 (30.2)	200.5 (27.7)	- 1.2 (28.8)	8.5 (27.4)	30.3 (19.0)
S3	160.0 (23.4)	164.0 (26.1)	184.1 (20.5)	202.3 (19.3)	205.4 (20.2)	- 9.9 (31.5)	1.4 (28.5)	- 3.7 (28.1)
Synchronize Condition								
S1	10.0 (19.3)	2.3 (19.8)	2.8 (20.6)	7.3 (19.9)	10.7 (20.3)	11.7 (22.1)	17.7 (21.7)	13.5 (23.8)
S2	- 6.5 (18.3)	- 1.5 (23.8)	3.7 (22.7)	10.0 (23.8)	19.4 (17.9)	25.9 (18.3)	34.6 (15.9)	41.6 (11.9)
S3	2.8 (18.6)	- 7.5 (17.0)	- 13.3 (21.7)	- 14.2 (23.8)	- 3.7 (26.2)	- 3.4 (26.6)	- 0.7 (25.8)	- 1.4 (28.0)

* Bold values correspond to syncopated coordination.

discussion]. They were then multiplied by a cosine-tapering window and transformed into the frequency domain with a discrete Fourier transform. Finally, power spectra were averaged across cycles in each data group and banded into four frequency bands: mu (8–12 Hz), low beta (15–20 Hz), high beta (20–30 Hz) and gamma (35–45 Hz). Resulting power values served as an estimate of the amplitude of each of these four neuromagnetic rhythms during task performance. To determine whether the mode of coordination had any effect on rhythm strength, we thus subtracted power values for the Syncopate condition from those of the Synchronize condition and converted the differences to z-scores. This procedure was applied for each plateau separately such that movement rate was not a contributing factor to observed differences between conditions. The spatial distribution of differences was assessed by topographically mapping z-scores (again on a 2D planar projection of known 3D sensor coordinates for each subject). Sensor z-scores that did not reach significance (after correction for multiple comparisons: 143 sensors) were set to zero before mapping.

RESULTS

Task performance

For low metronome frequencies, subjects were able to successfully time peak flexion in between successive beats in the Syncopate condition and on each beat in the Synchronize condition. At high metronome rates, however, all subjects showed a synchronized mode of timing regardless of the task condition replicating previous behavioral findings [Kelso et al., 1990]. In other words, once the rate of coordination became too high in the Syncopate condition subjects switched to synchronization to keep a 1:1 stimulus/response ratio as required by the task instructions. In general,

Subject 1 switched at a rate of 2.0 Hz (plateau 5) whereas Subjects 2 and 3 were able to maintain syncopation up to 2.25 Hz. Table I contains average relative phase values ($\pm$ SD) for each plateau from both coordination conditions. These values only reflect cycles kept for MEG analysis. Grand average relative phase values before and after the transitions in the Syncopate condition were 172.9° (± 23.7) and 12.7° (± 24.3), respectively. For the Synchronize condition, the average relative phase value across all plateaus was 6.7° (± 21.2).

Control conditions: dominant patterns of activity

Spatiotemporal decomposition of event-related fields from the control conditions yielded clear dipolar patterns for both the auditory (Fig. 1, left) and motor (Fig. 1, right) conditions in all three subjects. The auditory-related fields show bipolar activity bilaterally, presumably reflecting activation of the primary auditory cortex in each hemisphere. Motor-related patterns, on the other hand, consisted of a single dipolar structure in the left central region, corresponding to activation of the sensorimotor area (SM1) associated with movement of the right index finger.

Coordination conditions: event-related fields

We investigated both timing and amplitude characteristics of event-related field activity associated with each plateau from the two coordination conditions. At low plateau frequencies, event-related fields for all subjects were dominated by an auditory response field pattern occurring between 75 and 100 msec after tone onset (see yellow boxes in 1st and 3rd rows of Fig. 2 for example from both coordination conditions). This timing is consistent with the N1m, the primary magnetic auditory response [Näätänen and Picton, 1987]. Also observable was the P2m, the polarity reversal of

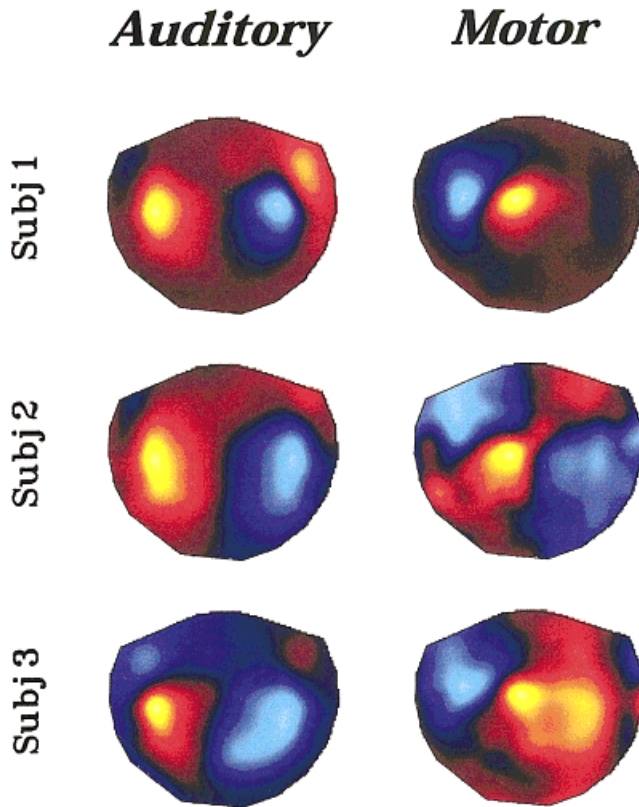


Figure 1.

Spatial patterns from a Karhunen-Loève decomposition that accounted for most of the signal variance in the event related fields computed from the Auditory (left) and Motor (right) control conditions. Blue/white and red/yellow indicate field lines entering and exiting the head surface, respectively. The head is viewed from above with the nose on top. All three subjects show dipolar structures that are bilateral in the auditory case and lateralized to the left side in the Motor case (reflecting movement of the right index finger). The amplitude here is in arbitrary units (because the patterns were obtained with a Karhunen-Loève decomposition).

this auditory component occurring approximately 70–120 msec later. Interestingly, these auditory field patterns were not observable at higher plateaus (e.g., see bottom two rows of Fig. 2).

The next strongest component in event-related fields at low plateau frequencies was a motor-related pattern that occurred during the flexion phase of the response. The strongest amplitude for this pattern actually coincided with the point of maximal *velocity* in the flexion direction, thus preceding peak flexion as previously observed [Kelso et al., 1998]. Due to the different timing of the response, this pattern emerges approximately one $\frac{1}{2}$ -cycle length after tone onset during syncopation and just before tone onset during synchronization (at about 307 and –57 msec in the Syncopate and Synchronize conditions, respectively,

for Subject 1's data in the top half of Fig. 2). The direct relation between the onset of this pattern and the motor response is further evident in the bottom half of Figure 2, which shows a portion of the event-related fields from a high frequency plateau (2.5 Hz). There is no difference in the onset of motor-related cortical activity between conditions (compare Figure 2, bottom two rows) because subjects were now synchronizing in both, i.e. the transition in the Syncopate condition had already occurred.

The timing of the motor-related pattern within each cycle can be tracked by plotting the phase of the coordination frequency component of the event-related field. This is shown in Figure 3, which plots this phase value for each of the eight plateaus from the Syncopate condition. The data shown are from Subject 1 who switched to synchronization at plateau 5 (2.0 Hz). Coincident with the transition on the behavioral level is a 180° switch in phase measures in left central sensors, thus replicating earlier work using a 37-SQUID array [Kelso et al. 1991, 1992; see also Daffertshofer et al., 2000; Fuchs et al., 2000ab]. Only sensors over the left sensorimotor area showed this shift (compare gray highlighted areas with motor field in Fig. 1). None of the other sensors show a clear-cut transition in phase that parallels the transition on the behavioral level (i.e., occurs at plateau 5). Figure 4 shows the same plot for data from the Synchronize condition. Because there were no changes in the timing of the motor response with increasing plateau frequency, the phase values over these same 'motor' sensors remain approximately constant. This phenomenon has also been previously observed in full-head EEG recordings [Wallenstein et al., 1995].

Amplitude differences in event-related fields were first examined by plotting total power of the MEG signal (Fig. 5). There was practically no difference in amplitude between conditions at any plateau rate as can be seen by comparing the bottom two rows in Figure 5. There were, however, interesting amplitude differences as a function of plateau rate. Signal power was initially concentrated bilaterally with a topographic distribution consistent with patterns of auditory activation (compare first columns of Figs. 1 and 5). As the plateau frequency was increased, the power decreased in these areas, especially in the right hemisphere, consistent with the lack of auditory field patterns in the event-related fields at higher rates. The remaining focus of power in the left hemisphere at high plateaus reflects the rate-dependent strengthening of the motor relative to the auditory response. Together these results indicate an interaction in frequency dependence of the auditory and motor-related

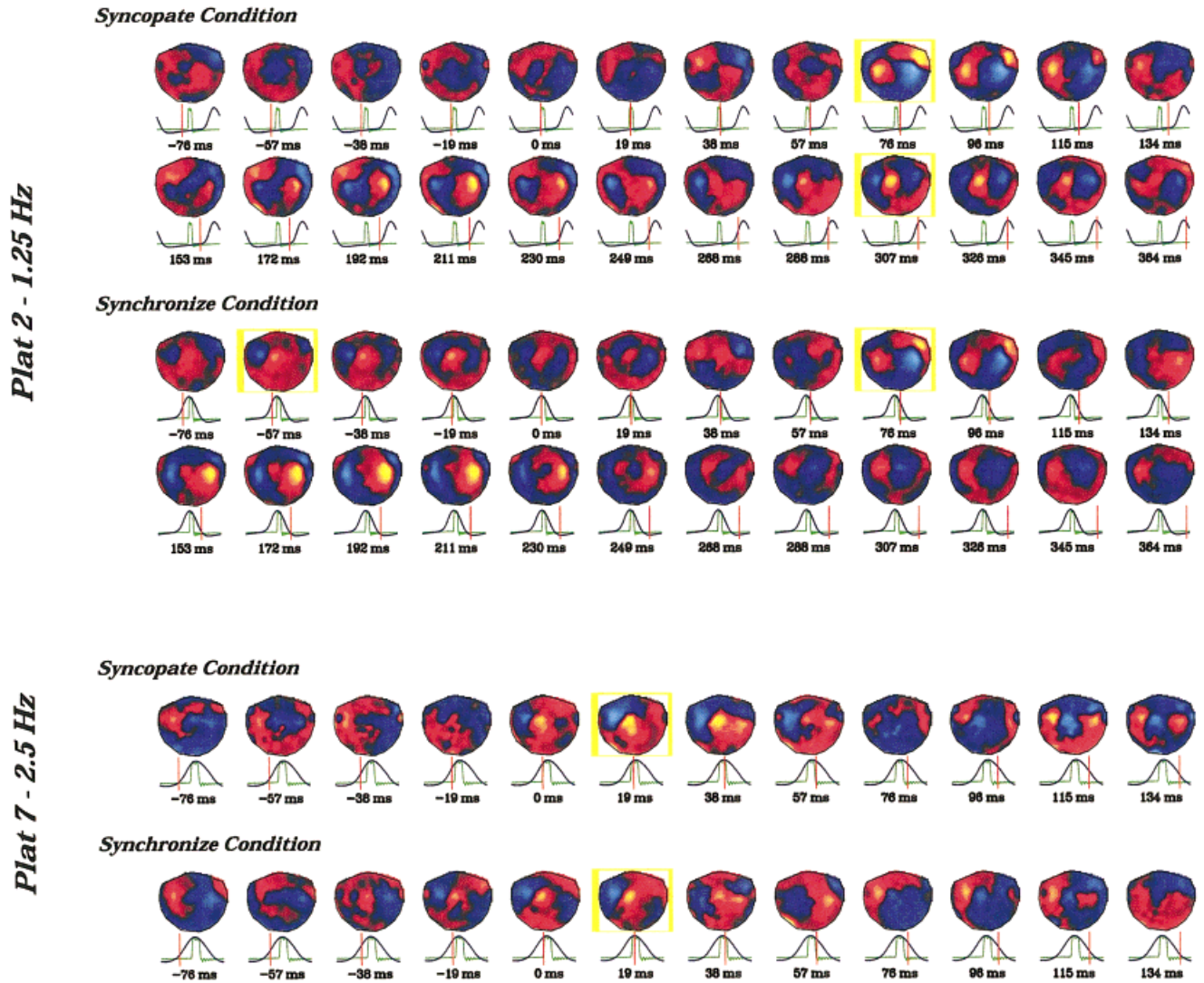


Figure 2.

Topographic maps sampled approximately every 19 msec from the event-related fields associated with a low (top half) and high (bottom half) frequency plateau from both coordination conditions. Data are from subject 1 but are typical for all three subjects. For plateau 2, maps are scaled to ± 227 and ± 290 fT for the Syncopate and Synchronize conditions, respectively. For plateau 7, the amplitudes are ± 133 and ± 107 fT. Green and blue lines show the corresponding averaged metronome and response time series, respectively, with the red line indicating the time point at which each map is sampled. Times given are with respect to the onset of

the metronome beat. Yellow boxes highlight the appearance of the two main patterns in each event-related field, the auditory and motor-related field patterns. Note that the motor field always occurs near the peak of the response and therefore at different times in the cycle for plateau 2 because the subject was syncopating in the Syncopate condition and synchronizing in the Synchronize condition. In contrast, for plateau 7 the timing of the motor field is the same for the two conditions, reflecting the fact that the subject was synchronized in both cases. See also caption for Figure 1.

contributions to the event-related fields. It is difficult, however, to discern whether motor areas have higher power at fast coordination frequencies because they show more activation with increasing rate or because their activation at low rates is swamped by the auditory response.

To obtain further insight into the relative contributions of auditory and motor-related processes to the event-related fields, we employed a dual-basis projection technique [Friedrich and Uhl, 1996; Fuchs et al., 2000b] in which the principal field patterns from the two control conditions were projected onto each

Syncopate Condition

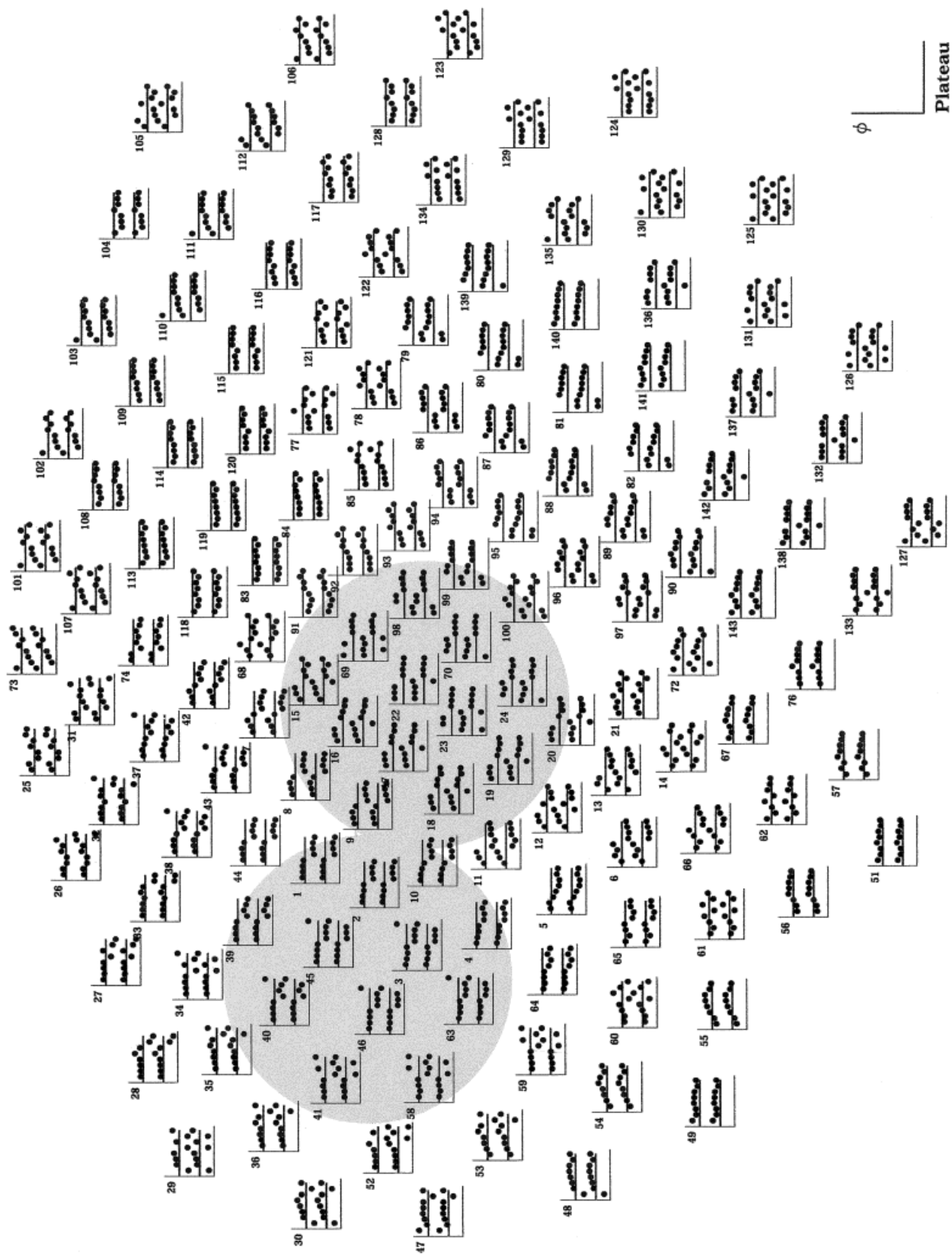


Figure 3.

event-related field. This projection resulted in time-dependent amplitudes for each pattern that reveal the patterns' temporal evolution in the event-related field. Together, the two control field patterns accounted for an average of 65% of the signal variance (across event-related fields from all plateaus) in both conditions. Figure 6 (top half) shows an example of auditory and motor time-dependent amplitudes (data from subject 1). Waveforms for the auditory pattern show a qualitative transition on plateau 4 at which point the N1m-P2m complex reverses in polarity. The motor pattern also shows a qualitative change characterized by a strong oscillation at about twice the cyclic rate at high plateaus that explains previous reports [Fuchs et al., 1992, 2000a,b; Kelso et al., 1992; see also Daffertshofer et al., 2000] of frequency doubling in the event-related field signal.

With respect to the amplitude of each component response as a function of plateau rate, all three subjects showed the same qualitative pattern in both conditions (Fig. 6, bottom). In the Syncopate condition, we observed a sharp decrease in the amplitude of the auditory response over the first four plateaus followed by approximately constant (or even gradual increases) amplitude levels throughout the rest of the trial. The contribution of the motor response, on the other hand, remained approximately constant across all eight plateaus. An interesting observation is the fact that the intersection of the two component curves occurs near the transition rate for each of the subjects. This explains previous results that demonstrated a topographic reorganization of the dominant pattern in the event-related field when subjects switched from syncopation to synchronization under conditions of increasing rate [Kelso et al., 1991, 1992; Fuchs et al., 1992]. For low plateaus, the event-related field is dominated by an auditory pattern whereas for higher plateaus the contribution of the motor-related pattern becomes stronger, even surpassing the auditory pattern amplitude for one of the subjects. Such rate-dependent change in the relative amplitudes of the auditory and motor responses may contribute to the behavioral transitions observed for this condition. Alternatively, they may be independent as is suggested

by the similar component amplitude curves obtained from the Synchronize condition (Fig. 6, bottom right). The auditory response curves in this condition, however, did not exhibit the sharp decrease in amplitude at lower plateau rates that characterized the event-related fields during syncopation. Rather they declined much more gradually, consistent with a more linear dependence on rate. This difference between conditions suggests that there may be differences in the way auditory information is processed when subjects are required to time movements between successive tones versus simultaneously with them.

Coordination conditions: task-related activity in higher frequency bands

A growing body of research associates changes in higher frequency bands with the performance of a variety of perceptual and motor tasks [Classen et al., 1998; Gray et al., 1989; MacKay, 1997; Pfurtscheller and Lopes da Silva, 1999; Vanni et al., 1999]. These high frequencies are not necessarily phase-locked to any task event and thus often average out if ensemble averaging is done in the time domain. We investigated whether MEG signal power in higher frequency bands differed depending on whether subjects were performing syncopated or synchronized coordination. Though spectral peaks were observed in the mu rhythm range (~ 10 Hz) and its first harmonic for both conditions, there was no difference in power at these peaks between conditions. This was true not only for contralateral sensorimotor sensors, but across the entire head surface. Gamma band (35–45 Hz) frequencies also showed no consistent significant differences in any area of the head. These results indicate that the neurons that generate mu and gamma rhythms are either not involved in performing syncopated or synchronized coordination or respond to parameters that are similar across the two conditions (e.g., movement duration, muscles activated, etc.).

In contrast, consistent significant differences between conditions were found in the beta range. These differences were broadband in nature ranging from 15–30 Hz. Figure 7 shows the topography of signifi-

Figure 3.

Phase of the brain signal with respect to tone onset versus plateau frequency (double plotted) in the Syncopate condition. Data shown are again from Subject 1 who switched to a synchronized mode of coordination at plateau 5. Sensor numbers are indicated in the upper left hand corner. The two lines indicate phase relationships of $\pm 180^\circ$. There is a clear 180° transition in sensors overlying left central areas (gray circles). The direction of the

transition (180° to 0° or vice versa) differs depending on the polarity of the event related field. No transitions are visible over other areas suggesting that the phase of the coordination frequency in the event related field tracks the shift of the motor response in time. Similar transitions were observed for the other two subjects who switched at plateau 6.

Synchronize Condition

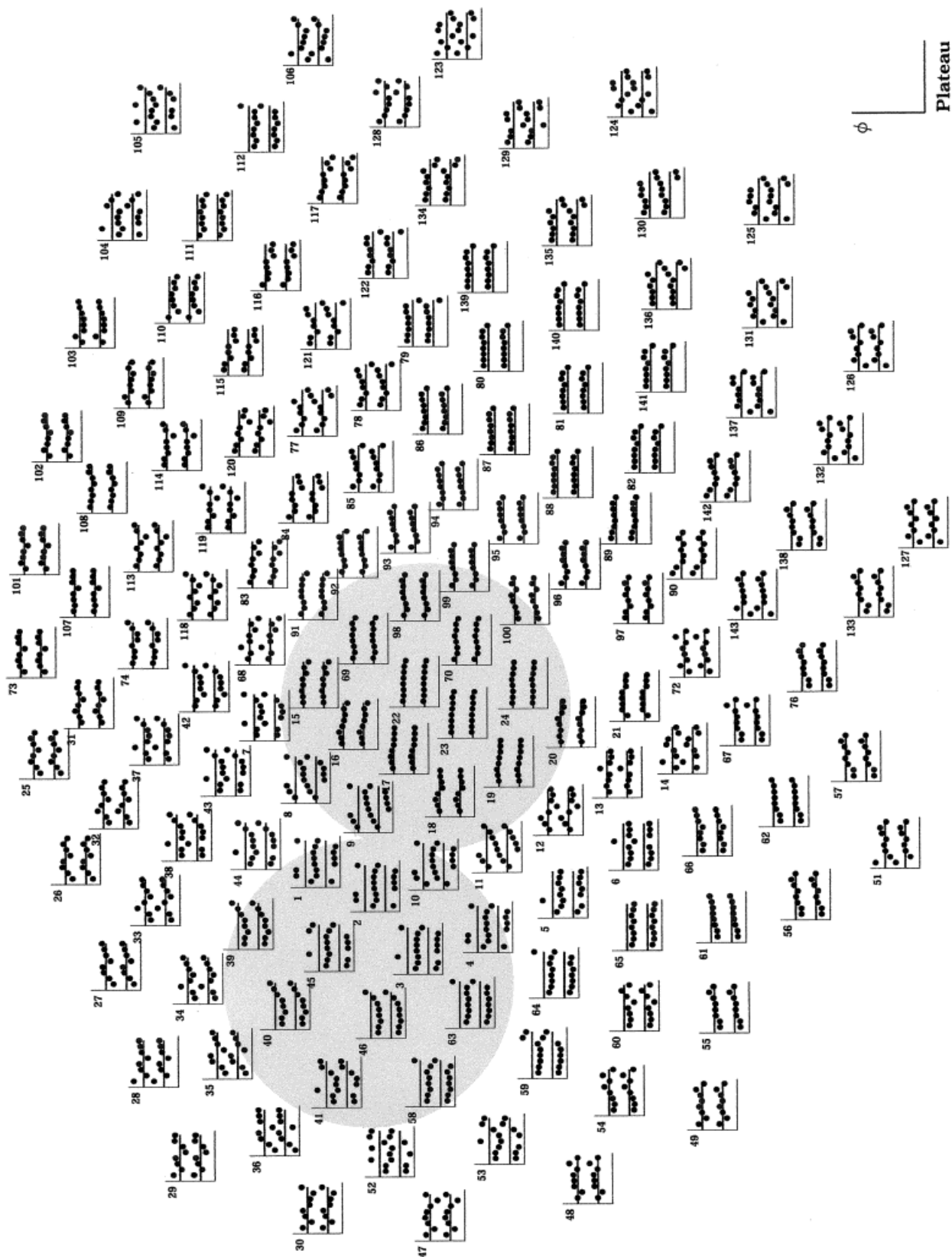


Figure 4.

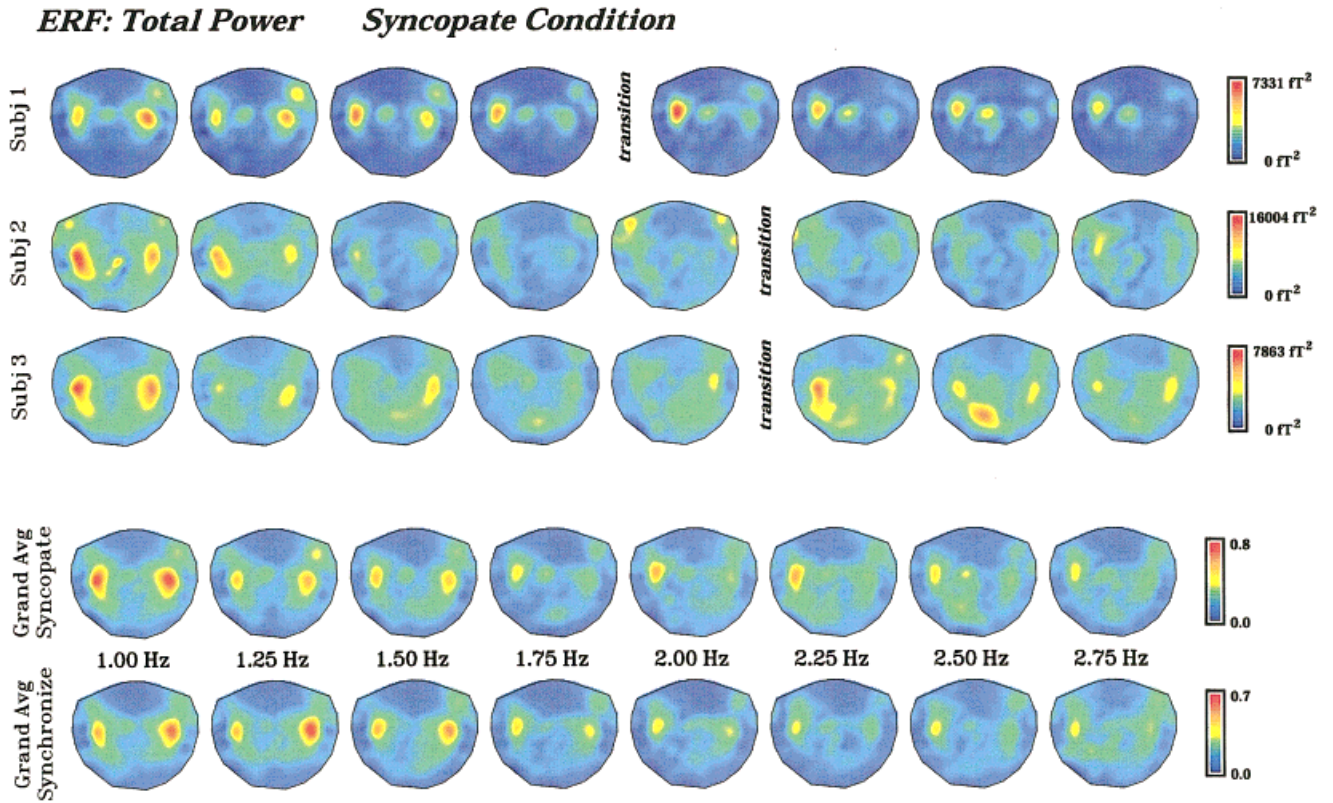


Figure 5.

Total power of the event-related fields (ERF) from the Syncopate condition for each subject. Each row is scaled independently. Grand averaged (normalized) data are shown on the bottom for both conditions. Initially power is concentrated bilaterally reflect-

ing the brain's auditory response but then decreases as the plateau frequency is increased. At high plateaus power is focused over the left side, associated with movement of the right finger. Note the similarity between conditions (compare bottom two rows).

cant differences in the 20–30 Hz range for all plateaus. Results from the 15–20 Hz range were nearly identical and are not included. Two observations are particularly relevant. First, before the transition in the Syncopate condition (indicated in the figure) there are highly significant differences in sensors over central and pre-central areas. These differences are concentrated over the left hemisphere (see enlarged map on bottom left) though they do extend across the midline and even into the right hemisphere. This suggests that activity in the contralateral sensorimotor cortex and perhaps also premotor (e.g., supplementary motor area) and ipsilateral sensorimotor areas changes in association with the mode of coordination. The second important observation is that, where there are differences, they are almost always in the same direction

with more beta power in the Synchronize condition. This indicates a greater suppression of beta activity during syncopation, the more difficult coordinative pattern.

A third interesting result was that even after the transition to synchronization, two of the subjects (Fig. 7, top two rows) continued to show significant differences in beta power over similar regions despite the fact that they were now synchronizing in both conditions. This suggests that the strength of the neuromagnetic beta rhythm depends not only on the mode of coordination currently being performed but also on previously performed coordinative patterns. In other words, there was a “carryover” or history effect of syncopation in the Syncopate condition that was not present in the Synchronize condition in which subjects

Figure 4.

Same as Figure 3 but for the Synchronize condition. Sensors that showed phase shifts in the Syncopate condition have a constant phase value across all plateaus reflecting the fact that the subject

was able to maintain a synchronized mode of coordination across the entire range of plateau frequencies. Data for all three subjects were similar.

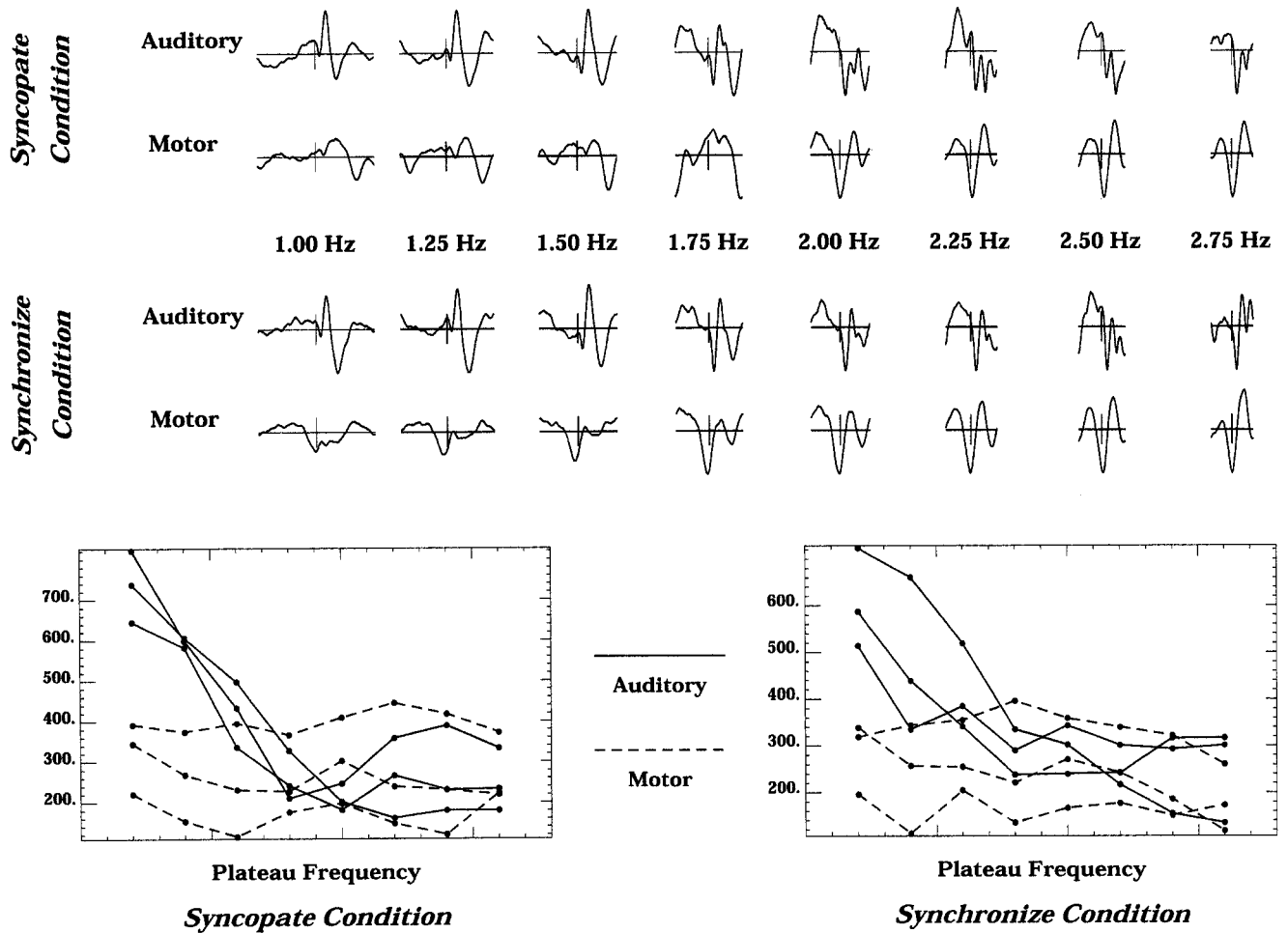


Figure 6.

Top half: Examples (from subject 1) of time-dependent amplitudes (TDA) of the auditory and motor-related field patterns calculated from a dual-basis projection procedure. Each TDA is independently scaled for ease of viewing. **Bottom half:** Maximum TDA amplitude (in arbitrary units) vs. plateau frequency plotted

for each subject and control pattern. All three subjects show a frequency-dependent decrease in the contribution of the auditory pattern to the event related field whereas the contribution of the motor pattern remains approximately constant throughout the entire run.

only synchronized with the metronome at all plateau rates. Together, these results suggest that neural populations responsible for generating beta rhythms in sensorimotor and premotor areas react to the way in which movement is organized in a given environmental context.

DISCUSSION

The strongest components in the event-related fields reflect auditory and motor-related activity. Furthermore, the characterization of these two patterns explains previous results [Fuchs et al. 1992, 2000b; Kelso et al., 1992] that demonstrate spatiotemporal shifts in neuromagnetic activity when subjects switch from

syncopation to synchronization with an auditory metronome in a ramped frequency task. Regarding temporal event-related field features, we have confirmed previous results [Fuchs et al., 1992; Kelso et al., 1991, 1992; Wallenstein et al., 1995] showing that 180° transitions occur in parallel on brain and behavioral levels in the Syncopate condition. We further show these transitions to be restricted to sensors that overlie contralateral sensorimotor areas. This topography plus the lack of transitions in the brain signals from the Synchronize condition suggest that the coordination frequency component of event-related fields (or potentials) tracks the timing of the brain's motor response (here signified by the motor field) within each cycle.

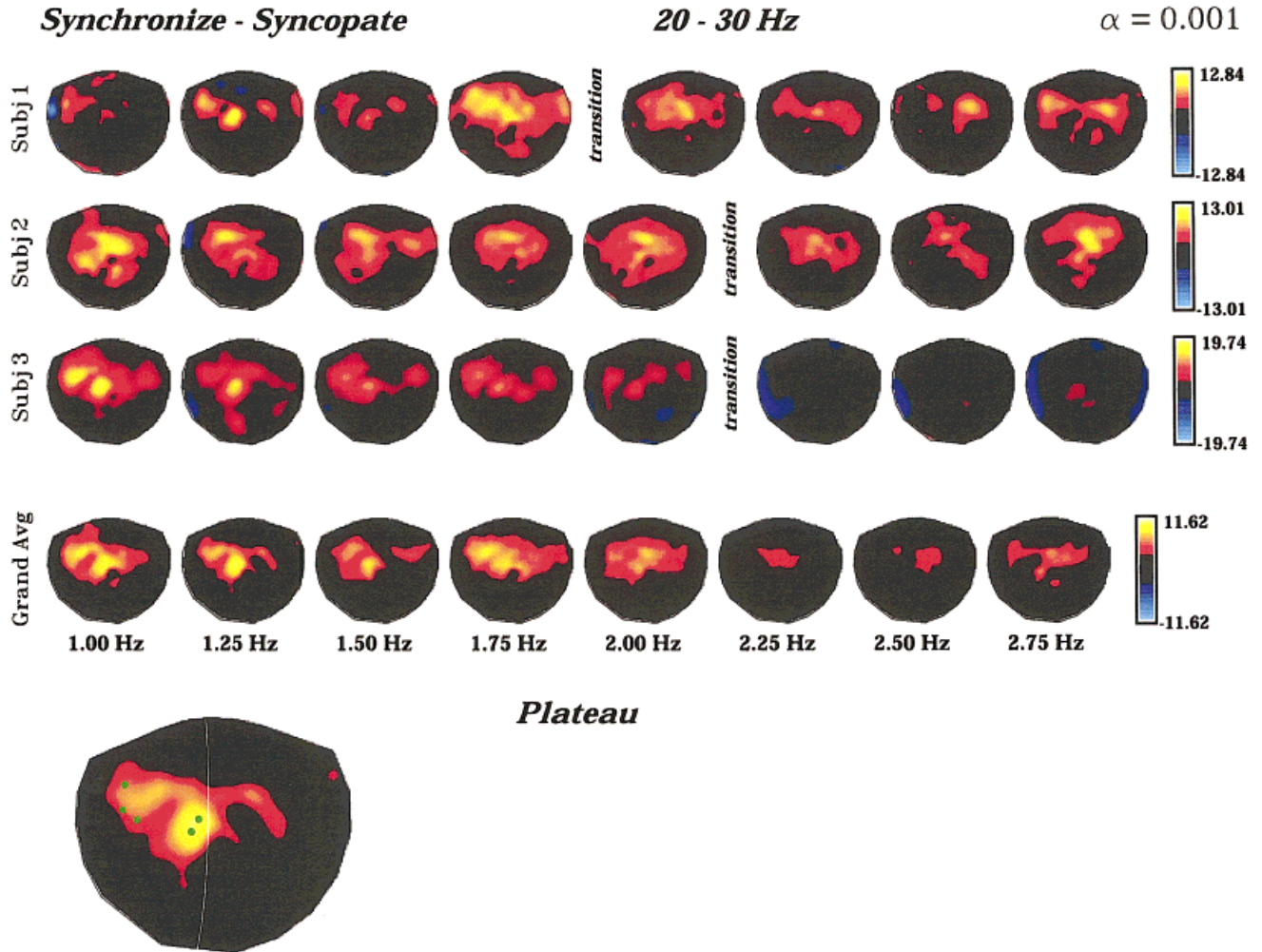


Figure 7.

Topographic maps showing areas of significant differences in MEG signal power in the high beta (20–30 Hz) frequency range for all three subjects and their grand average. Power values for the Syncopate condition were subtracted from those for the Synchronize condition. Maps of the 15–20 Hz range were similar and are not shown. The transition point is indicated for each subject; pre-transition the timing mode differed between the two conditions whereas post-transition subjects were synchronized in both cases. Difference values were converted to z-scores before plot-

ting; any z-score that did not exceed a confidence level of $\alpha = 0.001$ is shown as black. All differences are positive indicating that higher power levels were always found for the Synchronize condition. **Bottom:** Enlarged grand-averaged map from plateau I (1.0 Hz). White line connects sensors lying approximately on the midline and green dots correspond to sensors where the motor field amplitude was maximal and minimal in all three subjects (note that two subjects had minima at the same sensor location). There is a clear focus of differences over the left sensorimotor area.

Spatial reorganizations of activity previously observed with MEG recordings [Fuchs et al., 1992, 2000b; Kelso et al., 1992] can also be explained. Increasing the metronome rate leads to a decrease in amplitude of the brain's auditory response. On the other hand, the amplitude of the motor field is relatively unaffected by increasing coordination frequency. This interaction in frequency dependence causes low plateau neuromagnetic activity to be dominated by an auditory-related

pattern whereas for high plateaus, the strongest pattern is a motor-related dipolar field. There are at least two possible explanations for the decrease in amplitude of the auditory pattern. One is that after the transition to synchronization, a superposition of auditory and motor-related activity causes field cancellation. We reject this explanation because the same frequency-amplitude relationship is observed in the Synchronize condition during which the two re-

sponses are superimposed at all plateaus. A more likely explanation is a change in the way the brain processes auditory information.

The dependence of the brain's auditory response on inter-stimulus interval (ISI) is well known for both EEG [see Näätänen and Picton, 1987 for review] and MEG [Hari et al., 1982; Liu et al., 1998]. This phenomenon, however, has not been systematically investigated in the ISI range used here. Rather much of the work on auditory event-related activity has focused on either slower, transient evoked responses ($ISI > 2$ sec) or much faster steady-state responses (40 Hz) [see Lins and Picton, 1995 for review]. The range that affords syncopated or synchronized coordination is in the middle; it must be fast enough to allow anticipation of the next stimulus but still remain within the limits of biomechanical operation [see, e.g., Engström et al., 1996]. We speculate that the changes in auditory-related activity observed here reflect a transition to an increasingly steady-state response that results not only in the habituation of auditory cortical neurons, but also in a reorganization of sensorimotor integration networks leading to an inability to separate the motor response from each tone event. In other words, the motor response becomes entrained to the increasingly predictable series of tones, leading to synchronized coordination at faster metronome rates. Moreover, the decreases in auditory response amplitude throughout each trial in the Syncopate condition were characterized by a sharp decline before the behavioral transition to synchronization suggesting a nonlinear dependence on stimulation rate that contrasted with the more gradual decreases observed when subjects synchronized across all rates in the Synchronize condition. Though more subjects would be needed to statistically distinguish these two sets of curves, this observation may signify a difference in the way that auditory information is processed in the two situations. Such differences might not be surprising given that there is an overlap of tone arrival and movement for synchronization but not syncopation.

Neither the rate nor mode of coordination affected the amplitude of motor-related patterns of activity when event-related fields were examined. This is in contrast to previous analyses of EEG data that demonstrated differences in event-related potential signal power at the coordination frequency in electrodes over contralateral central and antero-parietal areas [Mayville et al., 1999]. Specifically, in Mayville et al. [1999] syncopation was associated with significantly stronger signal power at these sites when compared with synchronization at either the same or higher (e.g., post-transition) rates of movement. Though these dif-

ferences were not present in the event-related fields from the current experiment, frequency-averaging revealed significant differences in the power of beta oscillations (15–30 Hz) in sensors located over the same region, consistent with the hypothesis that activation of contralateral sensorimotor cortex varies with the coordinative pattern. Differences exist between plateaus 1–5 of each condition, the range of frequencies across which subjects syncopated in one condition and synchronized in the other. Unlike the EEG results, however, synchronized coordination was associated with significantly higher power than syncopation. This discrepancy in the direction of difference reflects the fact that in the former situation we examined time-averaged signal power at the coordination frequency whereas in this experiment we examined non phase-locked activity in much higher frequency ranges that is only preserved by averaging signals in the frequency domain.

Desynchronization of oscillations in the beta range during motor activity is a well-documented phenomenon in both EEG [Leocani et al., 1997; Pfurtscheller and Berghold, 1989; Pfurtscheller and Neuper, 1992; Pfurtscheller et al., 1996, 1998] and MEG [Hari et al., 1997; Kristeva-Feige et al., 1993; Salmelin and Hari, 1994]. Current theories posit that decreases in beta rhythm amplitude at the scalp signify a shift from an 'idling' state to task-related activation [Pfurtscheller et al., 1996; Pfurtscheller and Lopes da Silva, 1999]. Such amplitude changes, however, are typically defined with respect to baseline levels of activity associated with rest or some non-movement control condition. In our case, the ramped nature of the task precluded a comparison between each frequency plateau and some baseline period. Therefore we do not have a direct measure of how rhythmic activity changed in response to either type of auditory-motor coordination, i.e., whether it increased or decreased as compared with rest. Nevertheless, it is reasonable to conclude that the differences in rhythmic activity that we observe between the Syncopate and Synchronize conditions reflect similar differences in the functional organization of underlying neural networks. From this perspective, then, syncopated coordination is associated with a stronger event-related desynchronization (i.e., more task-related activity) than synchronization.

Changes in beta activity may, in some cases, reflect changes in mu rhythm oscillations to which frequencies in the beta range are harmonically related. Indeed, we observed peaks in the power spectra around both 10 Hz and its first harmonic. Neither peak differentiated between conditions, however, whereas both the low (15–20 Hz) and high (20–30 Hz) beta frequency

range, distinguished syncopated and synchronized coordination. This suggests that there are at least two distinct neuronal mechanisms associated with auditory-motor coordination, one that relates to the spectrally focused mu rhythm and one that generates broadband beta oscillations. Previous work in both EEG [Pfurtscheller et al., 1996] and MEG [Salmelin and Hari, 1994] indicates that mu rhythms are generated in somatosensory cortex whereas beta rhythms reflect activity in pre-central areas, including not only primary motor areas but also possibly premotor cortical areas. Our results are consistent with these studies. Because we are subtracting power between two conditions that both involve movement, it is not surprising that a rhythm generated in somatosensory areas (mu rhythm) shows no significant differences.

The observation of broadband differences in the 15–30 Hz range indicates that beta oscillations are generated by neural populations that respond to how motor behavior is organized within a given environmental context. This hypothesis is also supported by the fact that two of the three subjects in this experiment show a history effect; even after the transition to synchronization, these subjects still show a difference in beta power between conditions. Neural processes relating to movement generation or somatosensory stimulation cannot explain this result. Rather, the task context is the differentiating factor. In one case subjects have been synchronizing the whole time whereas in the other they have recently switched from a more difficult pattern. The former situation is certainly more automatic. Subjects establish a rhythm very quickly and thereafter must only attend to the modification of movement rate in response to perturbations introduced by increases in plateau frequency. In the Syncopate condition, however, subjects must also attend to the change in the timing pattern that accompanies the transition. In other words, they have to concentrate on reestablishing a 1:1 stimulus/response relation as required by the task in addition to modifying their coordination rate in response to perturbation.

One factor that is likely to differ with task context is the amount of attention/effort required to maintain a given pattern of sensorimotor coordination. Lower levels of beta power during syncopation (or post-transition synchronization) as compared with (transition-free) synchronization may thus reflect the fact that subjects must concentrate harder to maintain a syncopated mode of coordination. Although there is behavioral support for the hypothesis that syncopated (anti-phase) modes of coordination require more attention [Carson et al., 1999; Temprado et al., 1999], there is little evidence that scalp-recorded oscillations

in the 15–30 Hz range show stronger decreases in amplitude when the task condition requires more attention. A recent study by Manganotti et al. [1998] reports that beta (13–20 Hz) decreases tended to be stronger with motor sequences of increasing complexity but these differences were not found to be significant. The authors do state, however, that focal decreases in 16–19 Hz power were observed over contralateral centro-parietal regions. On the other hand, Murthy and Fetz [1992] showed that bursts of beta (25–35 Hz) oscillations in sensorimotor cortex were more frequent when monkeys performed a task that apparently required more attention and sensorimotor integration (reaching for a raisin vs. repetitive wrist flexion/extension). Such increases in beta activity are in contrast to the decreases we observe but could reflect differences between scalp and intracortical recording techniques. Whereas EEG and MEG activity measure the summed activation of many neuronal populations, microelectrodes pick up only local field activity. Increased arousal or action may act to split large synchronized neural populations into smaller functional groups that could simultaneously cause a decrease in amplitude of the aggregate signal measured at the scalp and an increase in oscillatory bursts within local populations.

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