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Neuromagnetic activity in alpha and beta bands reflect learning-induced increases in coordinative stability

K.J. Jantzen[a,*], Armin Fuchs[a], Justine M. Mayville[a], Lüder Deecke[b], J.A. Scott Kelso[a]

[a]Center for Complex Systems and Brain Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431, USA
[b]University Clinic of Neurology, Vienna, Austria

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Abstract

Objective: To investigate how learning induced increases in stability on a syncopation task are manifest in the dynamics of cortical activity.

Method: Magnetoencephalography was recorded from 143 sensors (CTF Systems, Inc). A pre-training procedure determined the critical frequency (F_c) for each subject ($n = 4$). Subjects either syncopated or synchronized to a metronome that increased in frequency from 1.2 to 3.0 Hz in 0.2 Hz steps. The F_c was the point at which subjects spontaneously switched from syncopation to synchronization. Subjects then underwent 100 training trials (with feedback) at F_c. Following the learning phase the pre-training procedure was repeated.

Results: An increase in the F_c occurred indicating that practice improved the stability of syncopation. The transition delay was also observed in the phase of the time-averaged signal in sensors over the contralateral sensorimotor area and in power analysis in the 8–12 Hz and 18–24 Hz frequency bands. Initially, reduced power was observed bilaterally during syncopation compared to synchronization. Following training, these differences were reduced or eliminated.

Conclusion: Pre-training power differences can be explained by the greater difficulty of the syncopation task. The reduction in power differences following training suggests that at the cortical level, syncopation became more similar to synchronization possibly reflecting a decrease in task and/or attention demands. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

In the last two decades transitions between behavioral states, hysteresis, multi-stable behavior and other related dynamical phenomena have been demonstrated both empirically and theoretically to be characteristic of, for example, speech categorization (Tuller et al., 1994), visual perception (Kelso et al., 1995; Hock et al., 1993; Ditzinger et al., 2000) and sensorimotor coordination (Kelso, 1984; Haken et al., 1985; Schmidt et al., 1990). Investigation of neural correlates underlying such phenomena is an active area of research using, for example, large electrode (Mayville et al., 1999; Wallenstein et al., 1995), and SQUID arrays (Kelso et al., 1991, 1992; Fuchs et al., 1992, 2000), as well as fMRI (Fuchs et al., 2000), PET and transcranial magnetic stimulation (Meyer-Lindenberg et al., 1999). Moreover, in a number of cases, it has been possible to derive the behavioral and neurophysiological effects from a theory based at the level of cortical neural ensembles and their intra- and inter-cortical connections (Jirsa and Haken, 1997; Jirsa et al., 1998; Kelso et al., 1999).

Somewhat counterintuitively, the paradigm that has been used successfully to probe the possible neural mechanisms underlying behavioral pattern formation and change focuses on instabilities. Instabilities prove to be important because they furnish predicted features of self organized dynamical systems (see Kelso, 1995; Haken, 1996 for reviews). A well-studied example is unimanual sensori-motor coordination. When subjects attempt to coordinate simple finger flexion movements with an external metronome in a syncopated pattern (anti-phase timing relationship) they can do so only at rates below approximately 2 Hz. As the rate of the metronome is further increased subjects experience a spontaneous switch to a synchronized (in phase) pattern. No such switch occurs when subjects begin in the synchronized mode (Kelso et al., 1990)

Previous neurophysiological studies have described several neural events correlated with these behavioral states and the transitions between them. For instance, transitions in

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* Corresponding author. Tel.: +1-561-2972230; fax: +1-561-2973634.
E-mail address: jantzen@walt.ccs.fau.edu (K.J. Jantzen).

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the relative phase (with respect to the metronome) of the averaged evoked fields (Fuchs et al., 1992, 2000; Kelso et al., 1991, 1992; Mayville et al., 2001 in press) and average evoked potentials (Wallenstein et al., 1995; Mayville et al., 1999) occur concomitantly with transitions in behavior. These phase shifts are seen predominantly in sensors overlying contralateral sensorimotor areas and are thought to reflect a switch in the timing between the motor evoked fields and pacing metronome (Fuchs et al., 2000; Mayville et al., 2001 in press).

A more recent investigation into the oscillatory responses of the brain associated with different coordination modes revealed a decrease in relative power within the beta range when subjects were required to syncopate as compared to synchronize (Chen et al., 1999; Mayville et al., 2001 in press). Task related decreases in power, have been well documented using both EEG and MEG (reviewed in Pfurtscheller and Lopes da Silva, 1999; Hari et al., 1997). Topographically organized desynchronization within the mu (Chatrian et al., 1959) and beta bands occurs at the onset of voluntary movement and remains until movement offset (Hari et al., 1997; Leocani et al., 1997; Pfurtscheller et al., 1997; Pfurtscheller and Lopes da Silva, 1999). Power decreases are observed over bilateral sensorimotor cortex but are dominant on the side contralateral to the movement (Leocani et al., 1997). Further, it has been demonstrated that increases in task complexity or attentional demands result in greater task-related power decreases (Boiten et al., 1992; Dujardin et al., 1993; Mangonotti et al., 1998). This leads to the possibility that the power differences reported by Mayville et al. (2001 in press) reflect additional task demands imposed by syncopation; a proposition that is consistent with behavioral evidence indicating that, compared to in-phase patterns, anti-phase coordination is less stable (e.g. Kelso, 1984; Kelso et al., 1986) and requires additional attentional resources (Carson et al., 1999; Temprado et al., 1999; Monno et al., 2000). Intention can also stabilize coordination states (Kelso et al., 1988; Scholz and Kelso, 1990).

One topic of interest within the context of coordination dynamics is the degree to which these intrinsically less stable patterns may be stabilized through learning. Learning within the realm of sensorimotor coordination has been shown to be a product of not only practice and experience, but also the dynamics of the pre-existing behavioral repertoire of individual subjects (Tuller and Kelso, 1989; Zanone and Kelso, 1992, 1997). Using a bimanual coordination paradigm, Zanone and Kelso (1992, 1997) showed that the stability of a specific phasing relationship was increased through learning. However, the change in stability of the phasing pattern to be learned was dependent on whether the novel task requirement competed or cooperated with the pre-existing behavioral pattern repertoire of each subject. Moreover, learning to produce a specific phase relationship between the fingers altered the stability (as measured by the variability of the produced phase relation) across a large range of possible phasing patterns, with the dual effect of increasing some previously unstable relationships and decreasing stability in previously existing patterns. Therefore, in order to adequately evaluate the learning process and its cortical correlates, it is important to have knowledge of the existing behavioral repertoire for each subject prior to learning. Learning, in the context of coordination dynamics, involves the modification of these pre-existing, so called 'intrinsic' dynamics (Kelso, 1995).

In this study we employed a novel method to investigate how learning alters the behavioral dynamics of unimanual sensori-motor coordination. The main idea was to use behavioral probes to map the stability of syncopation and synchronization at multiple movement rates both before and after learning. Subjects were trained to syncopate at the critical frequency at which they demonstrated a behavioral transition into synchronization as revealed by the initial probes. In this way, the behavioral training procedure was tailored to the pre-existing dynamics of each individual. We investigated whether practice at the critical frequency alters the threshold of switching from syncopation to synchronization and, if it does, how this increase in stability is reflected in the spatiotemporal properties of the cortical MEG. Given initial evidence that spectral power decreases are associated with the higher attentional demands of syncopation compared to synchronization (Mayville et al., 2001 in press), one might predict that as learning and experience act to stabilize syncopation at higher rates, these differences in power should decrease. That is, with learning the task demands associated with syncopation are reduced making it more akin to synchronization.

2. Methods

Neuromagnetic activity was recorded from participants during a set of procedures designed to: (1) determine baseline levels of stability during syncopated and synchronized coordination; (2) improve the ability of subjects to syncopate via a training paradigm; and (3) re-assess the ability of subjects to syncopate stably over a broader range of rates after training.

2.1. Subjects

A total of 4 right handed subjects (ages 31, 26, 33 and 28 for subjects 1 to 4, respectively) participated in this study. Informed consent was given by each subject prior to the start of any experimental procedures. All procedures conformed to the University's ethical guidelines.

2.2. Behavioral task

The experimental procedure was carried out in 3 phases: pre-training, training and post-training. In the pre-training phase subjects were required to perform two coordination conditions. They were instructed to either syncopate (produce finger flexion between successive beats) or synchronize (produce finger flexion on the beat) flexion of the right index finger with an auditory metronome. On each trial the rate of the metronome (1000 Hz tone, 60 ms duration) was systematically increased from 1.2 to 3.0 Hz in 0.2 Hz increments every 10 cycles (referred to as a plateau). Ten trials of each coordination pattern were performed. Subjects were further instructed to maintain a 1:1 relationship with the metronome by making a single response to each stimulus and to maintain this relationship even if they felt the coordination pattern begin to change. The syncopate condition was used as a baseline measure of coordinative stability since subjects are known to exhibit transitions to synchronization within this range of movement rates. The typical transition frequency was then used as the required coordination rate during training.

For the training phase, subjects were instructed to syncopate as well as possible to an auditory metronome presented at the critical frequency determined in phase 1. A single training trial consisted of 10 presentations (cycles) of the metronome. At the end of each trial subjects were presented with visual feedback about their performance. The mean and standard deviation (in ms) of the error was displayed on a computer screen placed several meters from the subjects. Trials were presented in 5 blocks of 20 trials each (1000 cycles total).

The post-training phase was simply a repetition of the first phase performed for the purpose of evaluating the effect of practice and training on the timing of the phase transition during syncopation. In both phase 1 and 3 the order of the different coordination trials was pseudo-random such that one condition could not occur on 3 consecutive trials.

2.3. Experimental procedures

During the experiment subjects were seated comfortably in a magnetically shielded room (Vacuum Schmelze, Hanau). The auditory metronome was presented binaurally through a set of plastic tubes. Subjects responded by depressing a lever that activated an optical switch, creating a single digital pulse for each flexion movement. This signal was recorded and processed during the course of the experiment to both determine the transition plateau for the purpose of setting the metronome rate for the training session, and for providing feedback during the training sessions. During experimental runs subjects were requested to fixate on a location on the computer monitor placed approximately 2 m in front of them and to restrict all eye blinks and other extraneous movements to the period between trials.

Neurophysiological data was collected during the pre- and post-training sessions using a magnetoencephalograph (MEG) consisting of 143 (141 were operational at the time of recording) first order gradiometers distributed equally throughout a helmet shaped dewar designed to cover the entire head (CTF Systems Inc, Port Coquitlam, Canada). Third order gradients were calculated online using a set of reference coils mounted within the dewar. All data channels, as well as the subject's responses were band pass filtered between 0.3 and 100 Hz online and notch filtered at the European line frequency of 50 Hz and its higher harmonics. Digitization was then performed at a rate of 312.5 Hz. The onset of the metronome was also coded on a separate digital channel. The location of the head within the dewar was determined via the digitization of 3 coils attached to the left and right preauricular points and the nasion. The location of the sensors within a head centered coordinate system could then be calculated.

2.4. Data analysis

2.4.1. Behavior

The timing relationship between the metronome and response was determined for each cycle and expressed as a relative phase. A single cycle was defined as the period between consecutive metronome beats. All responses (and the corresponding MEG data from that cycle) were classified as being either syncopated (180° ± 60°) or synchronized (0° ± 60°). Responses that did not meet either of these criteria were excluded from further analysis. Performance improvement was determined by comparisons of the actual cycle on which subjects switched into synchronization on each syncopation trial. This transition cycle was defined as the last syncopation cycle that preceded 5 consecutive non-syncopation cycles.

2.4.2. MEG

All MEG data were visually inspected and segments containing artifacts were marked and subsequently excluded from any further analysis procedures. Noisy channels were also noted and excluded. Individual cycles of MEG data were grouped according to coordination condition, metronome rate and the timing phase relationship. Average evoked fields were then calculated for each group. The time window for each average was equal to the period of the stimulus for the corresponding plateau and centered on the metronome. In general, between 80 and 100 cycles were included in each average.

In order to determine the timing relationship between the cortical response and coordination behavior, the phase of the brain response measured with respect to the metronome was investigated for the pre and post training sessions. The averaged neuromagnetic field was converted to the frequency domain using a Fast Fourier Transform (FFT) and the phase of the Fourier component corresponding to the metronome rate was then determined for each plateau. The resulting phase measures were then compared with the associated behavioral measures of relative phase.

The relationship between the coordination condition, the effects of learning and non-stimulus locked, higher frequency oscillations was also investigated. This was done by first removing the mean evoked field from each raw cycle of data before applying a 1/2 sine window function and calculating the power using an FFT. These individual power estimates were then averaged according to plateau and coordination condition and collapsed across two frequency bands: alpha (or mu) (8–12 Hz) and beta (18–24 Hz). Different conditions were compared by subtracting the power values for the syncopate condition from the synchronize condition at each plateau. To test for significance, these differences were converted to *Z* scores and Bonferonni-corrected for multiple comparisons (141 sensors). This procedure was carried out for pre- and post-training data sets. Significant differences ($\alpha \leq 0.005$) were displayed on topographical maps defined by a two dimensional projection of the actual sensor locations.

3. Results

3.1. Behavior

Fig. 1 shows the average pre-training (baseline) relative phase of the response for all subjects at each plateau. These averages were calculated using only the cycles in each plateau which were retained for MEG analysis as described in the Section 2. When subjects were asked to syncopate (closed circles) they were able to do so at lower metronome rates as indicated by relative phases near 180°. However, as the rate of the metronome was increased, all subjects spontaneously switched into synchronization (360°). This can be seen, for example, at plateau 7 (2.4 Hz) for subject 1 and plateau 6 (2.2 Hz) for subject 2. On the other hand, when subjects were required to produce movements that were synchronized with the metronome, they were able to maintain the pattern reasonably well at all movement rates. This confirms previous work showing a transition from bistability at low metronome rates (both syncopation and synchronization are possible) to monostability at higher rates (only synchronization is possible) (Kelso et al., 1990).

There were generally two effects of training on the subjects' ability to syncopate. Subjects were able either to delay the transition into synchronization, maintaining a syncopation pattern for longer than in the pre-training session (Fig. 2, top panel), or to completely eliminate the transition altogether (Fig. 2, lower panel). In the latter case, subjects were able to syncopate even at the highest metronome rate presented (3.0 Hz). Fig. 2 shows single trial examples of a delay in the phase transition for two subjects. Prior to training (open circles) subject 2 (top panel) maintained a near 180° phase relationship with the metronome until plateau 5. On this plateau a shift into synchronization occurred which was maintained for the remainder of the trial. Following training (closed circles) the same overall pattern was observed, however, the subject was able to maintain syncopation until plateau 7 before switching to synchronization. In the bottom panel subject 1 showed a pre-training transition on plateau 7 (open circles). However, after training this subject was able to maintain syncopation throughout the entire trial, never switching into the synchronization.

The mean pre- and post-training transition cycles for all subjects are shown in Fig. 3. All subjects showed a post training delay in the cycle on which the behavioral switch into synchronization occurred. In order to test whether the observed switching delay was statistically significant, we performed a two-way analysis of variance using subject and pre-post as factors. Significant main effects for both factors (subject $P < 0.0001$; pre-post $P < 0.0001$) as well as a significant interaction between them ($P = 0.015$) was observed. The interaction was analyzed via post-hoc one-

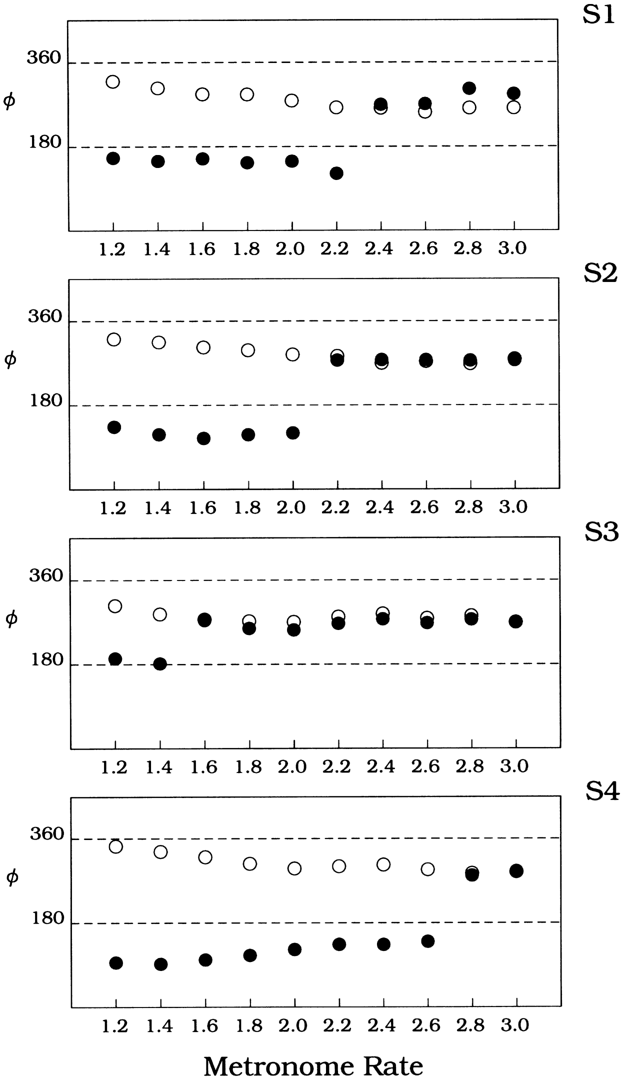

Fig. 1. Pre-training average relative phase as a function of frequency plateau for all 4 subjects. Each panel shows the average pre-training synchronization (open circles) and syncopation (closed circles) performance for a subject. Relative phase (expressed in degrees) was averaged across trials within each plateau (horizontal axis). All subjects showed a transition from syncopation to synchronization as a result of increasing the metronome rate. For subject 3 the transition occurred very early, between plateaus 2 and 3. No transitions were observed during synchronization, although there is a tendency to shift slowing with increasing rate.

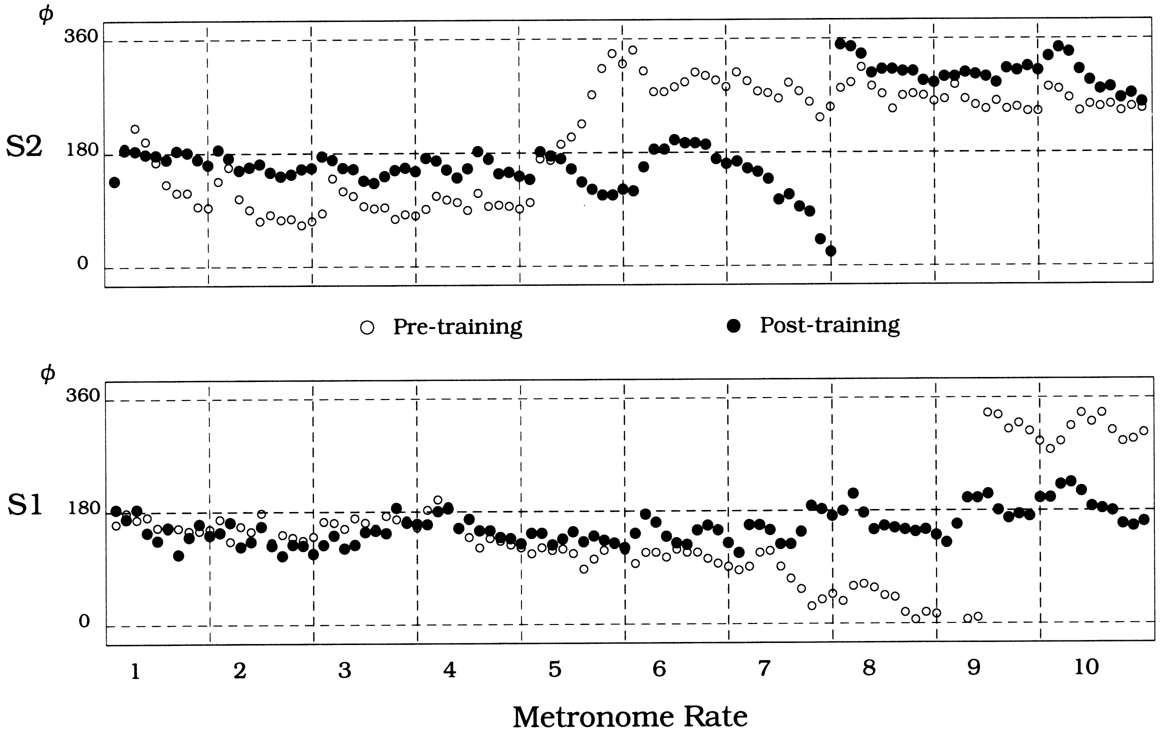

Fig. 2. Sample pre- and post-training relative phase for syncopation trials from subjects 2 (top panel) and 1 (bottom panel) plotted as a function of frequency plateau. Plateaus are marked with vertical dotted lines. The pre-training trials (open circles) show clear transitions to synchronization on plateaus 5 (2.0 Hz) and 7 (2.4 Hz) for subjects 2 and 1, respectively. After training (closed circles), subject 2 showed a delay in the onset of the transition into synchronization (plateau 7, 2.4 Hz). For Subject 1 the transition was eliminated and syncopation was maintained even at the highest metronome rates.

tailed *t* tests comparing the pre and post transition cycle data for individual subjects (the transition cycles from individual syncopation trials; results shown in Fig. 3). The *t* tests revealed that the interaction resulted from the fact that subjects 1, 2 and 4 showed significant improvement while subject 3 (although showing the same direction of change)

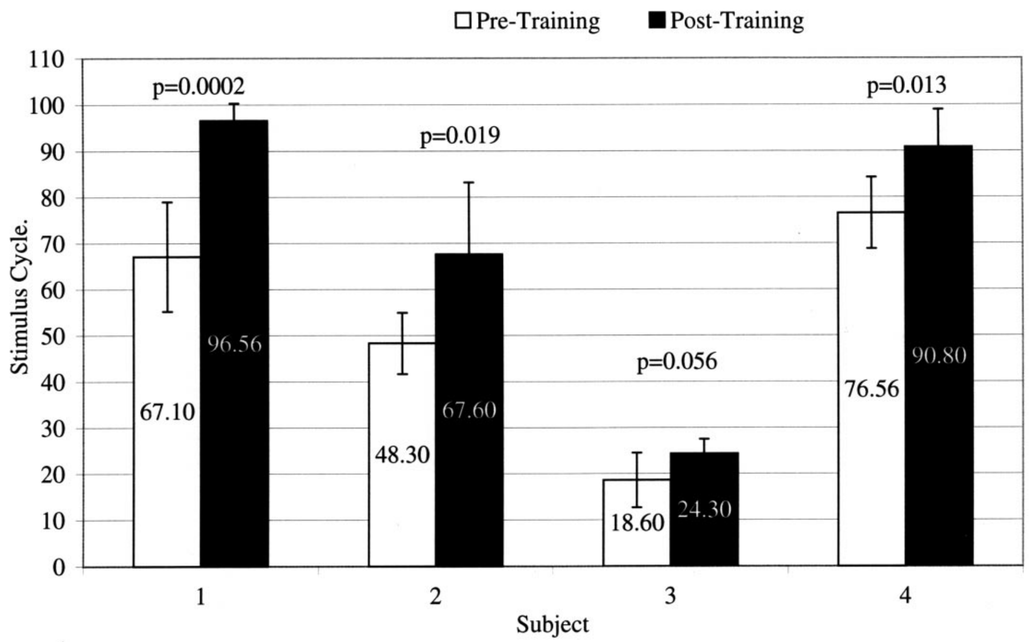

Fig. 3. Average pre- and post-training transition cycle for all subjects. Vertical bars show the average pre-training (white) and post-training (black) transition cycle. Error bars represent 95% confidence intervals. The *P* values listed above the data from each subject show the results of post hoc *t* tests.

did not improve significantly. These results show that training subjects to syncopate increased the stability of coordination over a larger range of metronome rates, thus allowing subjects to delay the transition from syncopation into synchronization.

3.2. Neuromagnetic activity

We investigated the relationship between the phase of the event related field (ERF) and the transition in coordination behavior described in the previous section. The phase of the pre-training ERF calculated with respect to the metronome frequency at each plateau is shown in Fig. 4. The data displayed are from the syncopation condition of Subject 2, who showed a transition into synchronization at plateau 5. Several sensors over the central-parietal area contralateral to the side of movement (shaded region) show a near 180° shift in phase that is coincident with the occurrence of the behavioral transition. At plateaus before the behavioral transition, these sensors show a consistent phase at either 180° or 360° (depending on the direction of the magnetic field) that switches at the transition plateau and remains consistent at its new value for the remainder of the plateaus. This result confirms previous reports of the relationship between the relative phase of behavioral movements and spectral phase of the average neuromagnetic activity (Fuchs et al., 1992, 2000; Kelso et al., 1991, 1992).

We further investigated if the timing of the phase transition in the cortical response (i.e., the movement rate at which the phase shift in the ERF occurs) corresponds to the improved ability of subjects to syncopate as a result of training. Fig. 5 compares the pre and post-training phases of the ERF. An isofield map of the average evoked field calculated from plateau one (movement rate 1.2 Hz) is shown in the center of Fig. 5. The dipolar-like nature of the field reversal over the contralateral sensorimotor region suggests an anteriorly directed dipole in sensorimotor cortex. This activation pattern is consistent with the post-MF reported by Gerloff et al. (1998) in a study investigating repetitive finger movements using MEG. The phase of the average evoked field on

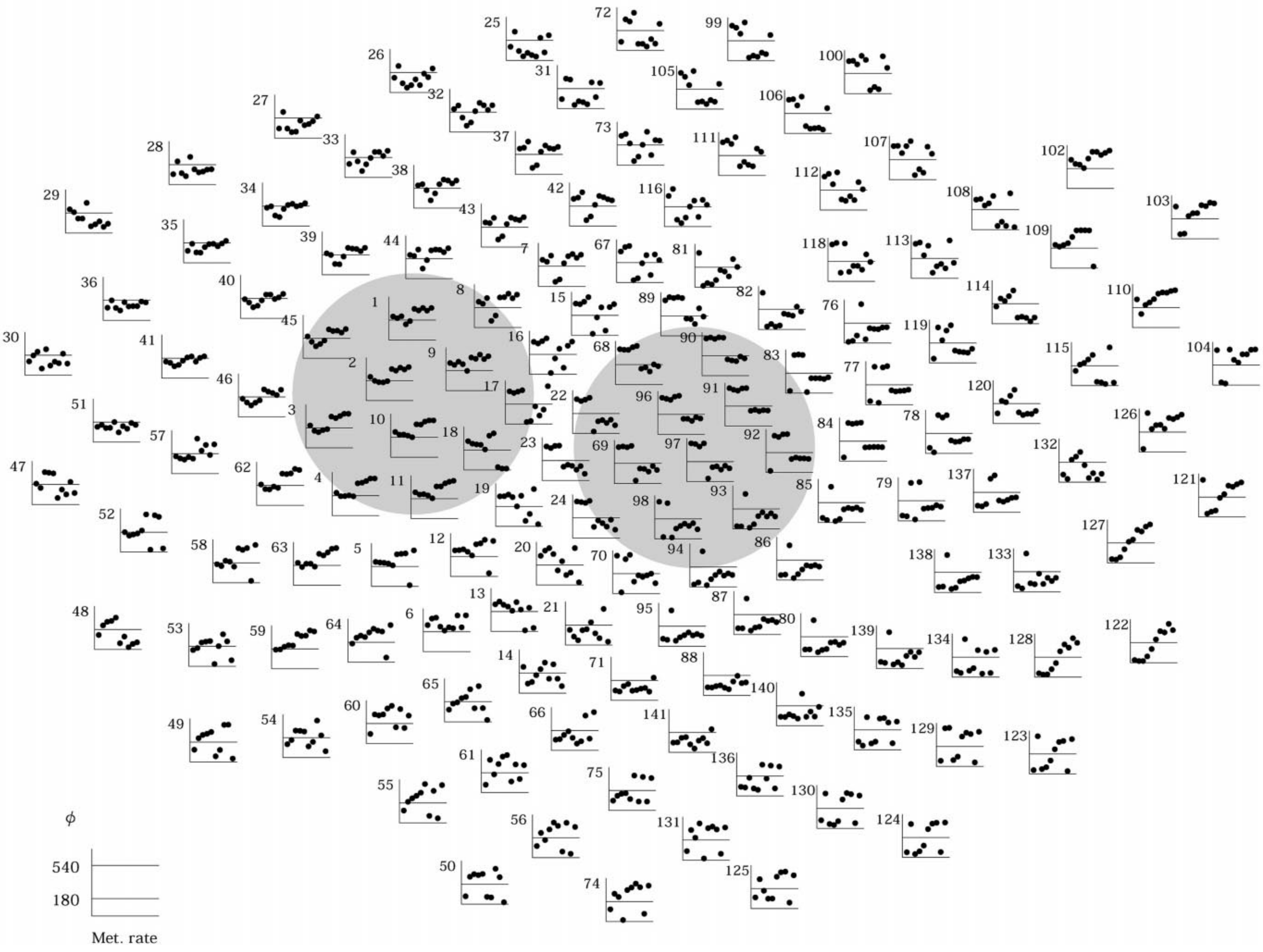

Fig. 4. Phase of the averaged syncopation evoked fields for the syncopation condition plotted as a function of plateau and according to sensor location. Horizontal lines indicate relative phase values of 180° and 540°. The data shown are from the pre-training session of subject 2. Switches in phase occurred in sensors overlying contralateral sensorimotor regions (gray ovals) on the same plateau as seen in the behavioral transition. The phase of the evoked field shows a clear transition from 180° to 0° (left oval) or from 0° to 180° (right oval). The inversions in phase is due to the dipolar nature of the evoked fields.

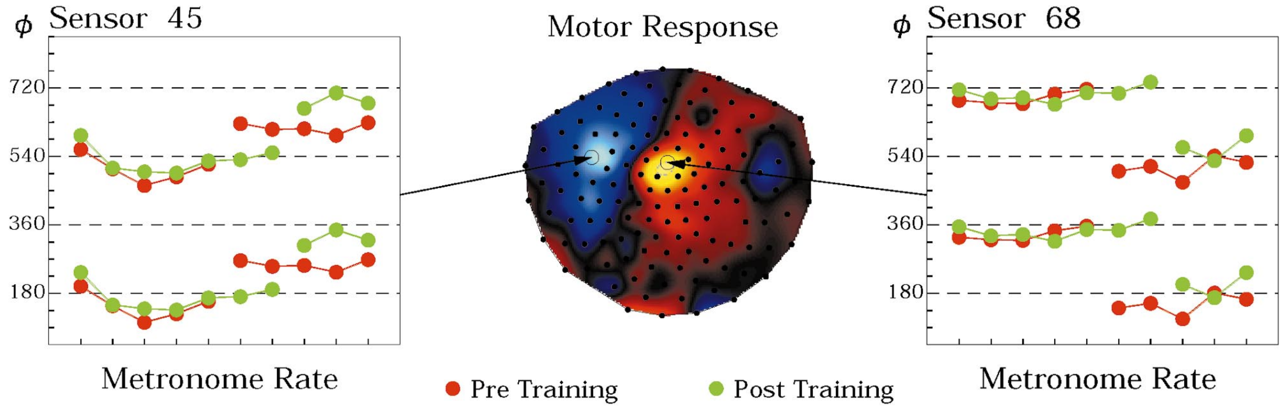

Fig. 5. Pre- and post-training comparison of the spectral phase of averaged evoked fields. Left and right panels show the phase of the averaged evoked field at each plateau calculated from both the pre- (red) and post- (green) training sessions. These sensors correspond to the maxima and minima of the motor-evoked field shown in the middle of the figure. This field distribution represents the activation pattern during motor responses and was generated using the average evoked field from plateau 1 of this subject. Both sensors show a shift in phase of approximately 180°. For both the pre- and post-training data, the plateau on which the shift occurs corresponds to the plateau on which the behavioral transition occurred.

each plateau is shown for two sensors that correspond to the maxima and minima of this evoked field pattern (arrows indicate sensor locations). The data shown are from the same subject as in Fig. 4 whose post-training transition was delayed until plateau 7. It is evident that both the pre-training (red circles) and post-training (green circles) cortical phase measures show a switch at the same plateau as observed in the behavioral data. The spatial location and specific timing of this shift is compatible with the idea that the phase of the ERF reflects the timing relationship between the cortical motor related activity and the external metronome. This concept is further supported by the discovery that learning-induced changes in the timing of the phase transition are also reflected in the phase of the ERF. These results not only confirm that there is a shift in phase in the cortical signal that tracks the timing of the behavioral transition, but also demonstrate that the cortical transition reflects training-induced behavioral improvements.

Averaged power spectra were used to investigate non-time locked neural activity related to learning to syncopate. Figs. 6 and 7 show the pre-training averaged spectra from Subject 2 plotted from sensors located over the contralateral (Fig. 6) and ipsilateral (Fig. 7) sensorimotor areas. The synchronization spectra (recorded during behavioral synchronization; dotted line) show bilateral peaks around 10 and 20 Hz which are much smaller over the contralateral hemisphere, consistent with other reported reductions in power within the mu and low beta bands during unilateral voluntary movement (see e.g., Hari et al., 1997; Mangonotti et al., 1998; Pfurtscheller and Lopes da Silva, 1999). Two main differences were observed when the subject was required to syncopate (solid lines). First, there was less power contralateral to the side of movement within both the 8–12 Hz and 18–24 Hz ranges. This appears to be primarily due to the near complete abatement of any spectral peaks at these frequencies during syncopation. Second, compared to synchronization, there was also a lack of power at these frequencies in the hemisphere ipsilateral to the side of movement (Fig. 7). Thus syncopation results in relative power decreases over bilateral central, temporal and parietal regions with a stronger reduction over the side ipsilateral to the movement. However, this larger relative difference in the ipsilateral sensors appears to be due mainly to greater power on this side during synchronization as opposed to a greater ipsilateral decrease during syncopation. Such a pattern is consistent with the notion that synchronization results primarily in contralateral power decreases whereas decreases observed during syncopation are bilateral.

Surface topographies of the significant differences ($P < 0.005$) between the two coordination conditions at each movement rate are shown in Fig. 8. Parts (A) and (B) show the pre- (tops rows) and post-training (bottom rows) differences in the 8–12 Hz and 18-24 Hz bands, respectively. In all cases where differences are observed, there is greater power associated with synchronization compared to syncopation (positive differences values). The existence of only positive power differences suggests either a consistent increase in power during synchronization or a decrease in power during syncopation. The latter is consistent with the findings of Mangonotti et al. (1998) who reported relative power decreases with increasing task demands or attention requirements. For the pre-training sessions, at plateaus prior to the transition, the power differences are concentrated over bilateral fronto-temporal areas. Such differences are more pronounced over the side ipsilateral to the movement, emphasizing our earlier observation that syncopated movement involves a reduction in power in bilateral motor cortices whereas power decreases during synchronization appear to be predominantly contralateral. Notice also in Fig. 8 that differences in power between synchronization and syncopation are greatly reduced or eliminated at plateaus following the behavioral transition. The fact that on all post-transition plateaus the subject was synchronizing in both conditions provides further support

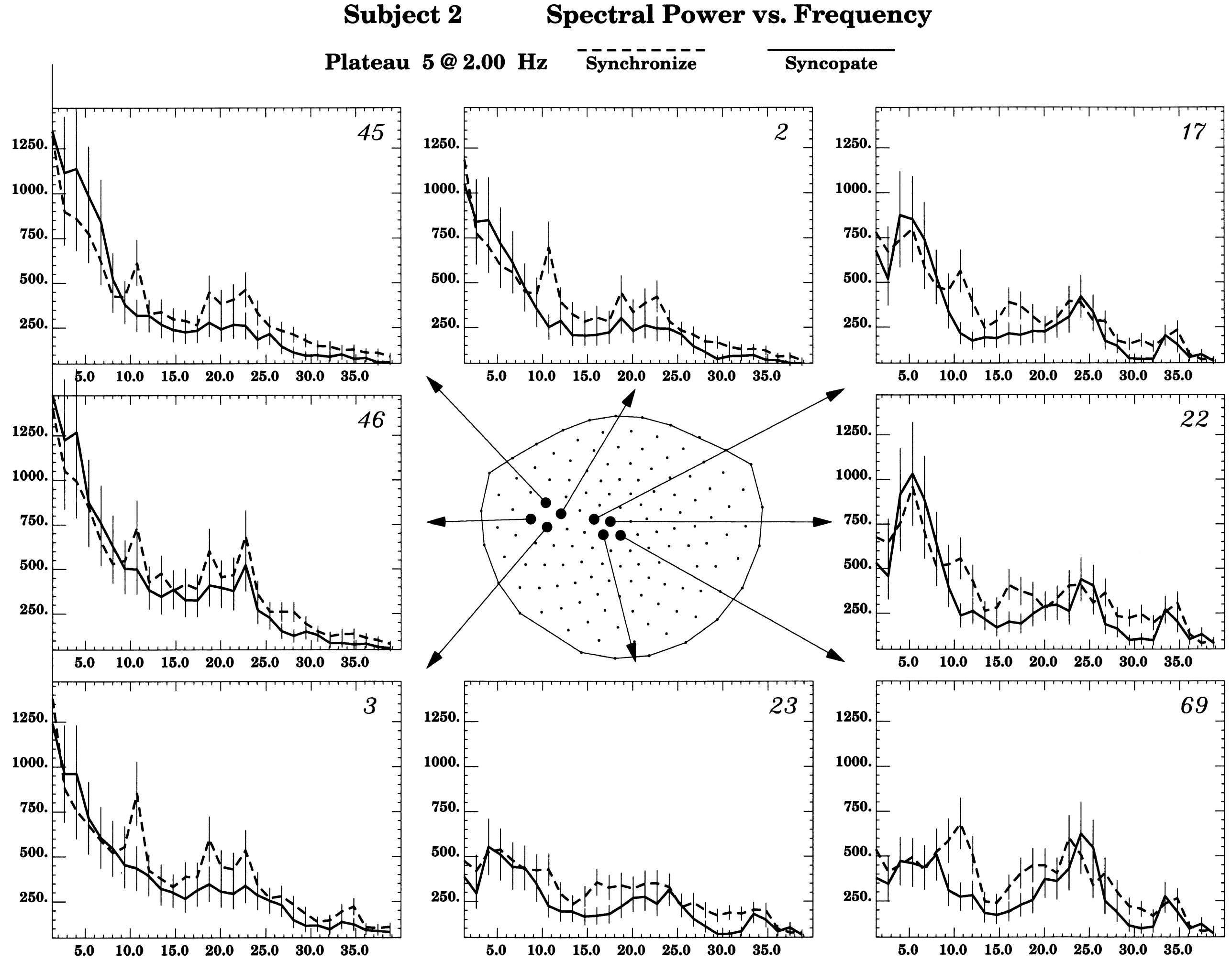

Fig. 6. A comparison of the average syncopate (solid lines) and synchronize (dotted lines) power spectra for a single subject from plateau 5 (2.0 Hz), prior to the behavioral transition. Each plot shows the spectral power (vertical axis) as a function of frequency (0–40 Hz, 1.34 Hz bin width, error bars show 95% confidence interval). The exact locations of the contralateral sensors generating these spectra are given by the highlighted dots on the sensor layout in the middle of the figure. Notice the spectral peaks near 10 and 22 Hz observed during synchronization which are reduced or absent during syncopation indicating a decrease in task-related power during the performance of the latter task.

that the observed power differences are related to task demands specific to syncopation.

Finally, we investigated how the training-induced delays of the phase transition are reflected in power differences between synchronization and syncopation. The post-training power difference maps are seen in the second row of each panel in Fig. 8A,B. Although the general pattern of power difference is similar to that seen during pre-training, the degree of difference is greatly reduced. This is reflected in both a reduction in the number of sensors showing a significant difference and also a reduction in the *Z* score at those sensors where differences were found. Thus, the decrease in power during syncopation observed prior to the training was not observed as strongly after subjects were trained to syncopate. As a result, the differences in power also no longer reflect where the transition from syncopation to synchronization occurred. Following behavioral training, oscillatory activity of the sensorimotor areas associated with syncopation appeared more similar to that observed during synchronization than prior to training. This change is summarized in part C of Fig. 8. The two plots show the grand average *Z* score at each movement rate for both the pre- (solid line) and post-training (dotted line) comparisons. Averages were computed across a subset of sensors covering sensorimotor cortex (inset in each plot) and across the 3 subjects who showed significant improvement on the task for both the 8–12 Hz (left) and 18–24 Hz (right) bands. The pre-training data show a large average *Z* score on those plateaus that precede the average behavioral transition (arrows). Following the transition the difference is greatly reduced or disappears altogether, reflecting the fact that subjects are now synchronizing in both conditions. Following training power differences in these early plateaus are either greatly reduced or eliminated showing no pre-post transition differences in average *Z* scores. It is also interesting to note that power differences are always relatively

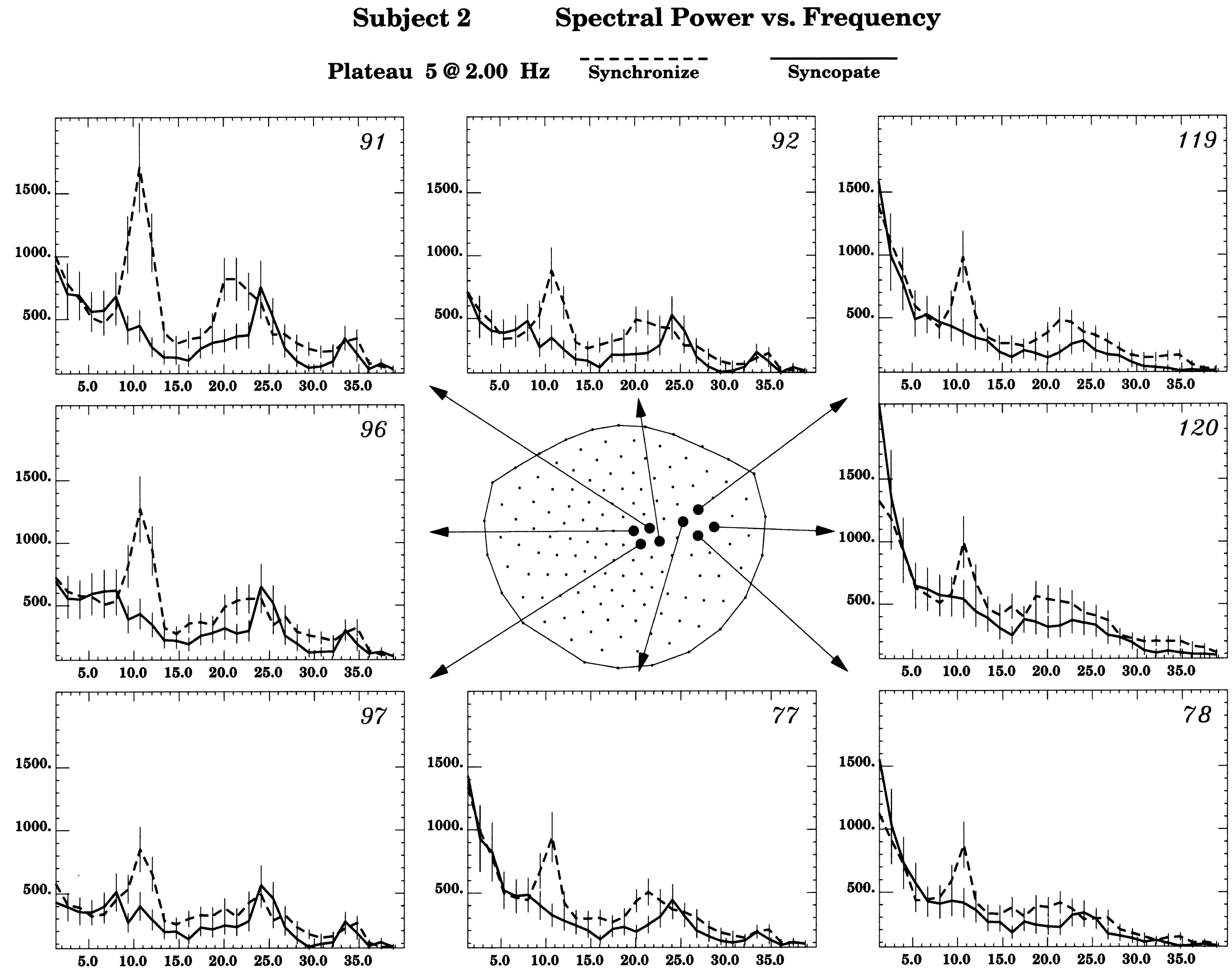

Fig. 7. A comparison of the average syncopate (solid lines) and synchronize (dotted lines) power spectra for a single subject from plateau 5 (2.0 Hz), prior to the behavioral transition. Each plot shows the spectral power (vertical axis) as a function of frequency (0–40 Hz, 1.34 Hz bin width, error bars show 95% confidence interval). The exact locations of the ipsilateral sensors generating these spectra are given by the highlighted dots on the sensor layout in the middle of the figure. The synchronization spectra have very prominent peaks at frequencies near 10 and 20 Hz. During syncopation there is a complete abatement of these peaks. This shows that power decreases associated with synchronization are restricted to the contralateral side, however, during syncopation the power in these bands is greatly reduced over both hemispheres.

small on plateaus 1 and 2. This may reflect the fact that at low metronome rates syncopation is relatively simple and therefore does not result in the same relative decreases in power observed in the later plateaus.

The fact that one subject did not show a significant delay in the transition from syncopation into synchronization allowed us to investigate whether changes in the oscillatory activity of the sensorimotor regions are related to improvement or merely practice. The *Z* score distributions within the 18–24 Hz band for this subject are shown in Fig. 9. As in Fig. 8, top and bottom rows show the pre-training and post-training differences respectively. Again there is a clear pre-training difference with more power over the sensorimotor areas during synchronization plateaus prior to the transition. In contrast to the other subjects, however, this same pattern is maintained after training. Although the figure indicates that the behavioral transition was delayed by one plateau, when expressed in terms of the transition cycles (see Fig. 3) this delay is quite small and, as shown earlier, is not significant. Thus it appears that changes in the oscillatory activity recorded during syncopation occur only under conditions where behavioral improvement occurs and are not merely a function of practice.

4. Discussion

Does learning to syncopate delay phase transitions in sensori-motor coordination, and, how are changes in cortical function related to changes in the behavioral dynamics? Our results show that practice produces a delay in the behavioral phase transition from syncopation into synchroniza-

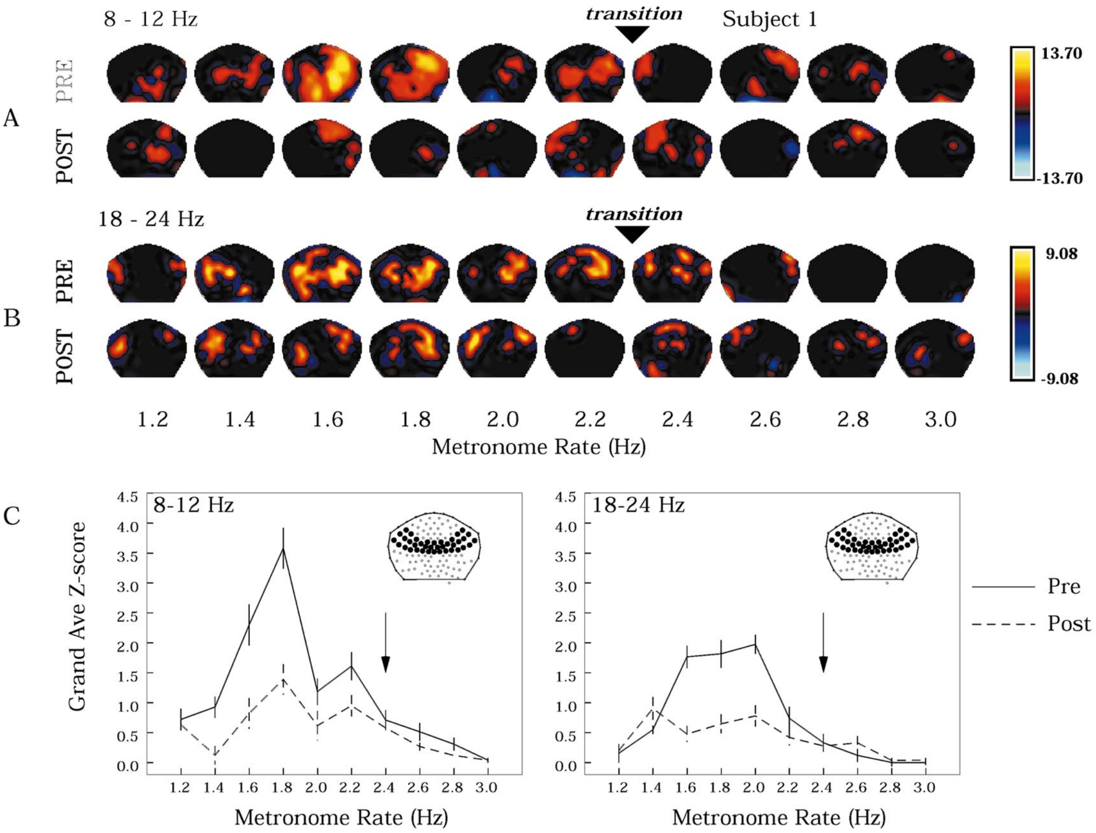

Fig. 8. Significant differences in neuromagnetic power between coordination conditions (synchronize minus syncopate) shown for pre- and post-training within the 8–12 Hz (A) and 18–24 Hz (B) range for subject 1. The topographic maps show the significant Z scores at each sensor ($\alpha = 0.005$). Each distribution is a projection along the z-axis of the sensors onto a two-dimensional surface such that the nose of the subject is at the top of each display. Color bars on the right show the range and direction of significant Z values. The behavioral transition is labeled and marked with an inverted arrowhead on each row. Pre-training power differences are concentrated over bilateral sensorimotor regions, with the largest differences occurring ipsilateral to the side of movement. Observed differences are strongest on plateaus before the behavioral transition. On later plateaus there is virtually no power differences between conditions. Following training, the power differences are greatly reduced when compared to those observed during pre-training, suggesting a change in the oscillatory properties of the brain that reflect improvement in syncopation. (C) Pre- (solid) and post-training (dotted) grand averaged power differences calculated for the 8–12 Hz (left) and 18–24 Hz (right) frequency bands. A grand average was calculated across the three subjects who showed improvement and across a subset of sensors (highlighted in the inset of each panel) for each required rate. In both frequency ranges the pre-training differences are large at slower, pre-transition rates. This difference is greatly reduced following the behavioral transition (marked by a vertical dashed line). After training, however, these pre-transition differences in power are either greatly reduced or eliminated.

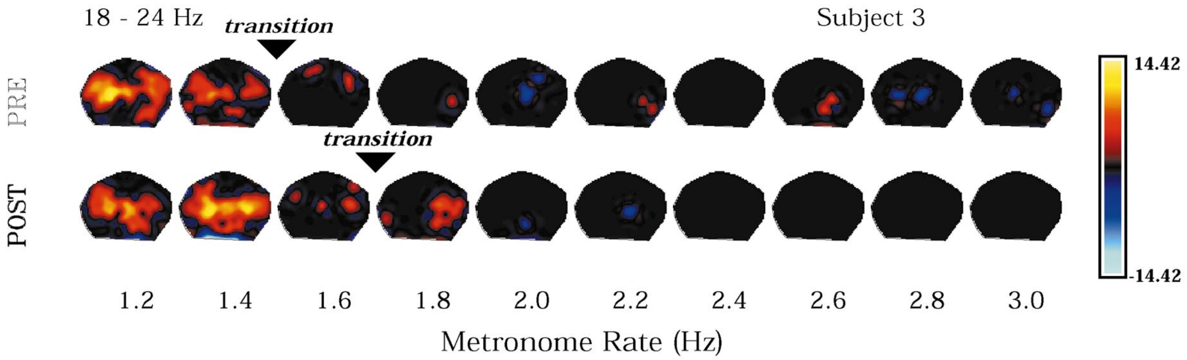

Fig. 9. Pre- and post-training spectral power differences within the 18–22 Hz range for subject 3. Conventions are the same as in part (A) of Fig. 8. This subject showed a very early behavioral transition and did not show a significant delay in the transition point as a result of training (e.g. Fig. 3). Pre-training spectral differences again show a decrease in power over bilateral sensorimotor regions during syncopation. This difference disappears following the behavioral transition. In contrast to other subjects, this subject continued to show this same pattern of spectral power following training suggesting that the changes in power are due to learning and not merely practice.

tion, perhaps by modifying intentional strength (Kelso et al., 1988; Scholz and Kelso, 1990). Behavioral improvement is correlated with a similar delay in a switch of the phase of the average evoked field, as well as a change in the amplitude and pattern of power changes in neuromagnetic activity within the alpha and beta frequency bands.

The coincidence in timing between behavioral transitions and shifts in the phase of the ERF reported here has been demonstrated previously (Kelso et al., 1991, 1992) and it has been suggested that the coincidence of these two measures reflects the relative timing between the motor related magnetic response and the occurrence of the auditory metronome (Fuchs et al., 1992, 2000). This is supported by our additional finding that the relationship between brain and behavior phase measures is preserved under conditions where the behavioral transition was delayed. The fact that the switch in phase of the event-related field also reflects the delay in the behavioral transition resulting from training would be fully predicted under the assumption that the motor-evoked response provides the main contribution to the frequency component at the movement rate. This measure therefore appears to be providing information concerning the existing phase relationship between the metronome and the movement on each plateau.

The pattern of relative spectral power differences observed in the current study is consistent with the phenomenon of event related desynchronization (ERD) described by Pfurtscheller and Aranibar (1997) (reviewed in Pfurtscheller and Lopes da Silva, 1999). Several authors have reported a decrease in power in the alpha and beta range during motor activity (Pfurtscheller and Aranibar, 1977; Pfurtscheller et al., 1997; Leocani et al., 1997) and have localized these spectral peaks to the primary sensorimotor regions, with the largest decrease contralateral to the side of movement (Hari et al., 1997).

Here we report a pre-training decrease in power within the mu and beta bands when subjects syncopate as opposed to synchronize with an external event. These differences are localized over bilateral sensorimotor areas and are largest over the ipsilateral side, due, we suggest, to an increase in bilateral desynchronization of neural activity during syncopation. Similar bilateral task related power decreases have been shown to occur with increasing complexity of a finger-sequencing task (Mangonotti et al., 1998). Whereas the latter authors report bilateral power decreases in all movement conditions, we have found it only for the more difficult syncopation task. This may be because even the simplest task in Mangonotti et al. (1998) was difficult enough to require some degree of attentional resources whereas the synchronization task used here can be performed virtually automatically. Mangonotti et al. (1998) suggest that bilateral decreases in power reflect an increase in the contribution of ipsilateral activation during more difficult motor tasks. Our observation of pre-training power differences only on pre-transition plateaus agrees with their conclusion. Once subjects experienced a transition into synchronization, power differences subsided, suggesting that the additional resources recruited during syncopation were no longer required, a finding in accordance with behavioral results showing that antiphase coordination requires more attention than in-phase coordination (Carson et al., 1999; Temprado et al., 1999; Monno et al., 2000).

Power differences between syncopation and synchronization evident during pre-training sessions were no longer observed after training. In general, the pattern and amount of post-training cortical desynchronization was very similar and was independent of the coordination mode performed, indicating that training not only resulted in a delay of the phase transition, but also altered the way in which the brain performs the task. This proposed connection between changes in the oscillatory activity of the brain during movement and a delay in the behavioral phase transition is supported by data from the one subject who did not show a delay in the phase transition: no differences were observed in the pre-post pattern of ERD.

The role that desynchronization of cortical rhythms plays in sensorimotor integration tasks such as that described here remains unclear. It has been suggested that ERD represents the activation of cortical networks for the purpose of information processing or motor production (Pfurtscheller and Lopez de Silva, 1997). An increase in the amount of ERD may indicate greater involvement of task specific cortical areas and the degree to which cortical areas are functionally connected. Our results suggest that a syncopated mode of coordination requires not only an increase in the activation of the same cortical areas required for synchronization, but also the additional involvement of ipsilateral regions. It is not possible to determine uniquely from the current results whether this represents a quantitative change within a common network or the activation of related sub-networks. However, the fact that the power distributions observed for both modes were very similar to each other following training (and the subsequent increase in stability of syncopated timing), suggests that both coordination modes are utilizing the same cortical network that is activated differentially depending on task demands.

Typically the calculation of event related desynchronization, as described by Pfurtscheller (Pfurtscheller, 1977; see also Pfurtscheller and Lopes da Silva, 1999), requires that the task related spectral power be compared with a ‘quiet’ baseline period. In the current study, however, an appropriate baseline period was not available for two reasons. Firstly, in our tasks, power changes occur in the context of an ongoing movement and are relative to those during the previous movement rates. Secondly, during the interval between successive trials subjects were allowed to move their eyes and make minor postural adjustments, precluding the use of this time period as a baseline indicator of spectral power in the MEG. Nonetheless, the indication that there is not only a power difference between the two modes of coordination, but that this power difference is alterable by practice (and presumably reflects learning) provides convincing evidence that desynchronization of oscillatory activity is an appropriate measure of learning and the associated allocation of attention. This possibility warrants the further investigation into the relationship between the frequency responses of the brain under various conditions (including different modes of coordination) within a framework that would allow for a more accurate determination of the absolute level of task-related synchronization under various manipulations such as learning, fatigue and distraction.

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