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EEG gamma-band phase synchronization between posterior and frontal cortex during mental rotation in humans

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Abstract

The main purpose of the present paper was: (1) to study the phase synchronization pattern in the γ-band while performing the classical Shepard–Metzler task of mental rotation; (2) to investigate the role of musical training; and (3) to study hemispheric differences in the degree of synchronization during mental rotation. Multivariate electroencephalograph signals from 20 male subjects (ten musicians and ten non-musicians) were recorded while performing the mental rotation task and also at resting condition. Phase synchronization was measured by a recent index, mean phase coherence. It was found that synchronization between frontal cortex and right parietal cortex was significantly increased during mental rotation with respect to rest, whereby musicians showed significantly higher degrees of synchronization than non-musicians. Left hemispheric dominance in the degree of phase synchronization, stronger in the posterior right parietal and occipital regions, was observed in musicians. Right hemispheric dominance was generally observed in non-musicians. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

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Mental rotation is a widely discussed concept that suggests an analogous mode of visual information processing in certain visuospatial cognitive tasks. This task, originally introduced by Shepard and Metzler [16], demands discrimination between the image and mirror-image of rotated 3D objects, for which human subjects need an increasing reaction time depending on the angular disparity between the rotated objects. Other than behavioral results, one great interest in the study of mental rotation is the neural mechanism underlying the task. Imaging studies indicated the primary activation in parietal cortex with additional co-activations in premotor and supplementary motor areas while performing mental rotation [3,12,18,19]. An electroencephalograph (EEG) study found activity over the left premotor regions and other areas of the frontal cortex [20] and ERP based results indicated a marked negative component over the right frontocentral region [7]. Further, the question of cerebral asymmetry during mental rotation demands a lot of attention; an early imaging study reported right hemispheric dominance [6], whereas no clear differences were found by some later studies [4,18]. These different results suggest that mental rotation like any other complex cognitive function is performed by a host of sub-processes working synchronously while sub-processes are being carried out in different cortical areas [4]. In this study, we addressed the problem of finding the synchronization pattern in the γ-band while performing the classical mental rotation task as compared with resting state. The γ-band was chosen because there are numerous evidences that neuronal oscillations and synchronization in the high frequency γ-range (> 30 Hz) provide a general framework of large-scale cognitive integration [13,17]. A recent index was used to detect phase synchronization (or synchrony, used interchangeably), which was found to be robust for noisy and non-stationary time series [9].

Beside the topic of gender differences [11,19], another interesting but unresolved debate in this context is the possible correlation between musical training and spatio-temporal reasoning [10]. Based on a model incorporating the columnar organization of cortex, it was predicted that musical training would enhance performance in some spatial tasks [8]. Therefore, we compared the degrees of synchronization between musicians and non-musicians while performing mental rotation and at resting condition.

The four figures used in the task of mental rotation were

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similar to the original figures [16]. Subjects were requested to answer by 'yes' or 'no', whether or not the two figures were identical. In the control state, subjects were looking at a white wall. In other studies, identical or mirror-rotated figures were used as a control condition but there was a chance of induced carry-over processing effects from the experimental to the control stimulus condition because the subject might try to mentally rotate also the control stimuli due to similarity in shape and outline as the experimental stimuli. Thus in the present study, the overall neuronal dynamics during mental rotation was maximally emphasized by choosing a control condition requiring minimal cognitive demand. Spontaneous EEG signals were recorded from 20 right-handed male subjects (ten musicians, mean age 25.7 years, each with at least 5 years of musical training, and ten non-musicians, mean age 25.4 years with no musical training) by 19 electrodes (Fig. 1) with a sampling frequency of 128 Hz and A/D precision of 12 bit. Average of signals from the two ear-lobes was used as the reference.

The general condition [14] for phase synchronization between two coupled non-linear oscillators is defined as:

$$\varphi_{n,m} = |n\phi_1(t) - m\phi_2(t)| < \alpha$$

where n and m are positive integers, $\phi_{1,2}$ are the phases of two oscillators, and α is an arbitrary constant. The instantaneous phase of any signal $\{x(t)\}$is:

$$\phi(t) = \tan^{-1}\frac{x_H(t)}{x(t)}$$

where $\{x_H(t)\}$ is the Hilbert transform of $\{x(t)\}$. After finding the instantaneous phases ($\phi_{1,2}$) of individual signals and their phase differences ($\psi = \phi_1 – \phi_2$, $m = n = 1$) between two signals of length L, the index to characterize the strength of phase synchrony is defined as:

$$R = \left|\frac{1}{L}\sum_{t=0}^{L-1} e^{i\psi(t)}\right|$$

which was called mean phase coherence [9]. This index (R) can efficiently detect the phase synchrony between two systems even when their amplitudes are completely uncorrelated. The higher the value of R between two EEG channels, the stronger the degree of phase synchronization and the stronger the functional coupling between cortical areas associated with these two channels. R was computed using a window of 6 s with overlapping segments of 5.875 s; within each window 171 values of R were produced considering all possible combinations between 19 electrodes. For the evaluation of significant differences in R between the task and resting condition and also between groups, paired Wilcoxon tests were applied. The rank sums obtained were converted to error probabilities which were schematically presented in probability maps.

Fig. 1 shows the pattern of enhanced synchronization during mental rotation as compared with resting condition for all subjects. Several noteworthy features have to be mentioned. First, the topographical enhancement was quite symmetric in the two hemispheres. Secondly, within each hemisphere, phase synchrony was strongly increased between parietal (P3, Pz, P4) and frontal (F3, Fz, F4) areas and posterior temporal areas (T5, T6). Moreover, these latter areas showed enhanced synchrony with midline electrodes (Cz, Fz). Frontopolar (Fp1, Fp2) to frontobasal (F7, F8) connections were also enhanced. Thirdly, contralaterally, the synchronization between occipital, parietal, and frontal regions was significantly increased. In addition, phase synchrony was also higher between frontal areas of each hemisphere.

When repeating the results by comparing the task vs. rest within each group, a similar kind of topographical pattern was produced although the number of enhanced connections was much higher for musicians.

Fig. 2 shows the comparison between the two groups while performing mental rotation. It is explicit that the degree of the γ-band synchrony in musicians was significantly higher than in non-musicians; the enhancement was found over multiple cortical areas reflected by dense patterns in musicians as compared with the total group (Fig. 1), the pattern of connections was tighter in the left hemisphere. On the other hand, in non-musicians phase synchrony values associated mostly with right temporal regions were found to be higher than in musicians. It should be noted that no large significant differences were found between the two groups at resting condition [2].

We also studied the variations of the time course of phase synchrony within each hemisphere (Fig. 3) for both groups. In musicians, the left hemisphere presented stronger phase synchrony than the right one (Mann–Whitney rank-sum test,

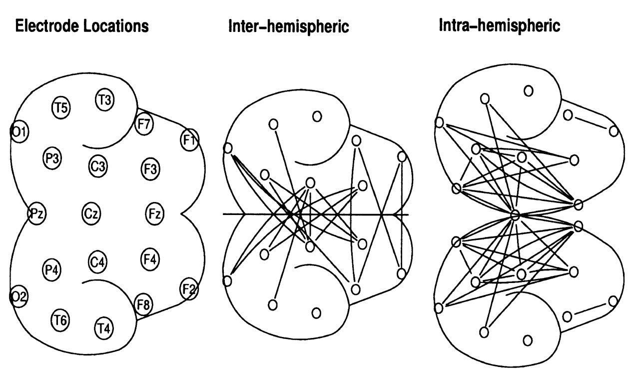

Fig. 1. Left: Spatial position of the 19 electrodes and their designations according to the international 10–20 electrode placement system. Middle & right: Topographical representations showing significant increases in the degree of γ-band phase synchrony for performing mental rotation compared to the EEG at rest for all 20 subjects. Paired Wilcoxon tests were used as statistical filters and two electrodes were joined by lines if the associated error probability $P \leq 0.01$. For the sake of clarity, two hemispheres are displayed separately to show intra-hemispheric connections (right). Phase synchronization between posterior areas, primarily parietal cortex, and frontal cortex turned out to be greatly enhanced during mental rotations.

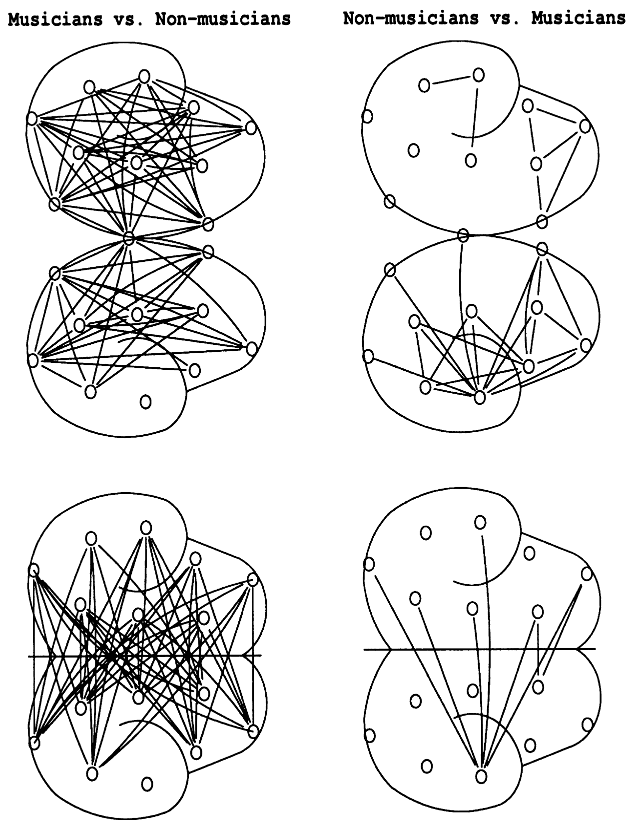

Fig. 2. Significant probability mapping showing the comparison (in the degrees of the γ-band phase synchronization) between musicians and non-musicians while performing mental rotation. The left column shows the increase for the group of musicians and the right for non-musician (See Fig. 1 for electrode locations). Musicians showed extensive increase of phase synchrony between multiple cortical areas, manifested as short and long-range connections, as compared with non-musicians.

$Z = 20.85$, $P < 0.001$), whereas an opposite hemispheric dominance, i.e. right, was found in non-musicians ($Z = 30.30$, $P < 0.001$). The variations in synchrony with time within each hemisphere were similar for musician (Pearson's product-moment correlation coefficient, $r = 0.49$), yet much less for non-musicians ($r = 0.30$).

The process of mental rotation is primarily composed of three main steps: (i) visual perception of both objects; (ii) mental rotation of the object; and (iii) decision whether or not both objects are identical. The occipital cortex is primarily responsible for visual processing, the parietal cortex, mainly its right superior parietal lobule, for the spatial processing and the prefrontal cortex as a whole for holding the relevant information with necessary updates and finally yielding the decision [1]. This study clearly shows that the functional coupling between posterior parietal cortex and frontal cortex was significantly enhanced for all subjects while performing mental rotation as compared with resting condition. Further, the strong synchronization observed in the frontopolar and frontobasal regions is consistent with a dominant role of frontal eye fields, mostly in control of occulomotor function in scanning the visual objects [4]. Long-distance interaction between frontal and posterior association areas was found in the θ-band (4–7.5 Hz) in tasks demanding spatial short-term memory [15], which also plays an implicit role in this task of mental rotation. However, on repeating the whole analysis in the θ-band, no long-range phase synchrony between posterior and frontal areas was found. Musical training was earlier reported to enhance the performance of tasks related with spatio-temporal reasoning [10] and verbal memory [3]. The most conspicuous finding here is the type of cerebral asymmetry in the two groups: musicians showed significant left hemispheric dominance in the degree of synchrony, whereas non-musicians showed right hemispheric dominance throughout the entire time course, which is in agreement with previous imaging studies [5,6]. Left-hemispheric dominance for musicians was also found while listening to music [2]; generally, the left hemisphere is better suited for tasks demanding higher analytical reasoning. The opposite hemispheric dominances due to different strategies in each group are most likely the reason of the symmetric pattern (Fig. 1) for the combined group result.

We would like to stress here that the present study does

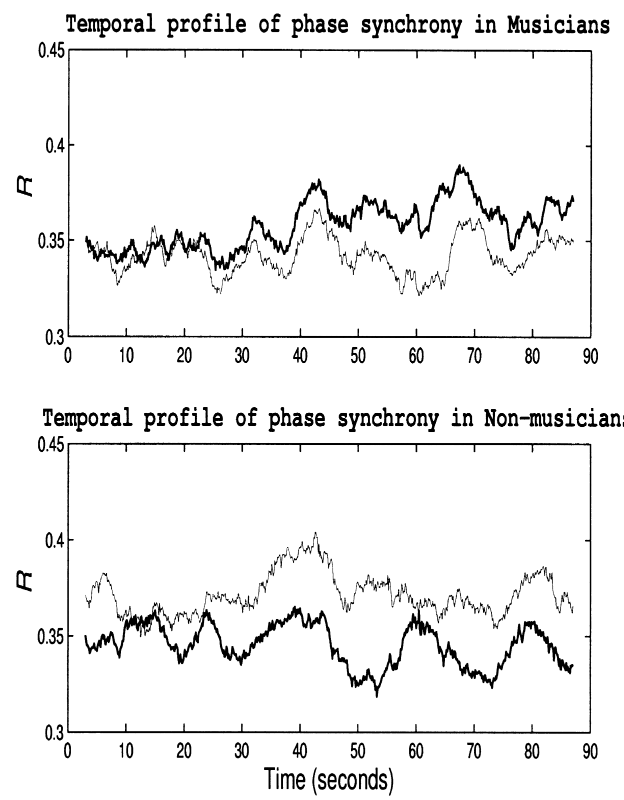

Fig. 3. Temporal variations of phase synchrony (R, see text for details) in the γ-band for the two groups: musicians (upper figure) and non-musicians (lower) during mental rotations. Results were averaged over all subjects within each group and all possible electrode combinations as follows: within left hemisphere (thick line), within right hemisphere (thin line). In musicians, the left hemisphere was more synchronized than the right one; the effect was opposite in non-musicians.

not allow conclusions from the degree of synchronization on the performance or efficiency in the task.

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