Gender dependent EEG-changes during a mental rotation task

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Abstract

This study is based on 30 students, 15 females and 15 males. EEG was recorded with 19 electrodes according to the international 10/20 system against averaged signals picked up from both ear lobes. Averaged power spectra and cross-power spectra between all electrode-positions were computed. Data were reduced to five frequency bands (theta, alpha1, alpha2, beta1 and beta2) and finally mean amplitude and coherence were computed. EEG-recordings were made during a mental rotation task (Shepard-figures). The obtained spectral parameters were compared with the corresponding values of a baseline activity with eyes open at rest. The results of statistical evaluations (paired Wilcoxon tests, Wilcoxon tests of independent samples) were presented in error probability maps. In males, local coherence decreased between the posterior left electrodes in the theta-band. In females, a decrease of coherence between the posterior right electrodes were observed in this frequency-band. In contrast to females, males showed an increase of coherence between frontal, central and parietal electrode positions in both hemispheres in the alpha1-band. The increase of local coherence in the beta1-band over the right temporo-parietal sites in the male group was more pronounced than in the female group. Especially in females, interhemispheric coherence increased between the posterior electrodes in the theta-, beta1- and beta2-ranges. This study suggests the involvement of many brain areas during mental rotation. Females show a rather symmetrical allocation of coherence increase in theta, beta1 and beta2.

Keywords: EEG-amplitude; EEG-coherence; Mental rotation; Imagery; Sex differences; Probability mapping

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1. Introduction

The idea that gender differences exist in the functional brain organisation during different cognitive abilities has been confirmed by many investigators (McGlone, 1980; Butler, 1984; Kimura and Harsham, 1984; Kimura, 1992). Generally, visual spatial functions are represented in the right hemisphere and verbal functions in the left. Especially, the right parietal lobe is important during visual performance in normal subjects (Kolb and Whishaw, 1990). However, the competence of each hemisphere in processing different cognitive performances were also investigated in split-brain patients (Blance-Garin et al., 1993; Perez Trullen et al., 1993; Baynes et al., 1998).

Unilateral or bilateral representation of different cognitive functions could depend on the different sizes of neural fibres that connect the two hemispheres in the two genders. The posterior part of the corpus callosum could be a reflection of the interhemispheric axonal differences between both genders (deLacoste-Utamsing and Holloway, 1982; Kimura, 1987; Adler, 1989; Witelson, 1989; Allen et al., 1991). Accordingly, it was concluded that females have a more bilateral brain organisation than males and so the interhemispheric transfer of information over the larger corpus callosum is more effective in the women’s brain (McGlone, 1980; Bryden, 1989; Springer and Deutsch, 1989).

Concerning the cortical representation of cognitive functions and particularly spatial abilities it was argued that spatial performances are optimised when these abilities are strongly lateralised in one hemisphere (Levy and Negylinki, 1972; Levy, 1976). Psychological tests revealed that in the average females scored higher in most tests of verbal abilities whereas males scored higher in visual spatial abilities. Levy’s Cognitive Crowding Hypothesis (1976) could explain gender differences in verbal and spatial abilities. Levy pointed out that bilateral representation of verbal abilities in females seems to support verbal skills because of the involvement of greater neural masses. Females also tend to involve both hemispheres during the solution of spatial tasks. One reason could be that women use verbal strategies when solving spatial tasks. This could be associated to a better communication between the two hemispheres, which contribute to verbal fluency. Thus, the advantage in females in verbal fluency could be due to the larger and more efficient corpus callosum (Hines, 1990). According to Levy’s Cognitive Crowding Hypothesis (1976) females range lower in the performance of spatial skills because bilateral representation is not the optimal cortical organisation for spatial tasks. So, the cortical involvement of one or both hemispheres depends on the task per se.

Beside the differences in strategies and in the cortical representation in both genders there is general agreement that visual spatial ability is not a homogenous construct. Linn and Peterson (1986) analysed different visual–spatial tests whereby three factors emerged: spatial perception, mental rotation and spatial visualisation. Thus, the comparison of different tests needs to be interpreted with caution. The reported gender differences strongly depend on which component of visual spatial ability is measured. In this regard, Farah (1989) showed that different components of imagery processing such as mental imagery and mental rotation are differently lateralised. Mental images generated in memory depend primarily on structures in the posterior left hemisphere. In contrast, the rotation of mental images primarily depends on structures in the posterior right hemisphere. In a PET study Kosslyn et al. (1997) found that during visual perception and visual imagery different areas were involved. Fourteen areas were activated in both tasks. Two regions were activated in perception but not imagery, and five were activated in imagery but not in perception. Data by Hoptman and Davidson (1994) reveal, that when both hemispheres have some competence at a difficult task, there is a benefit to interhemispheric interaction. Kosslyn et al. (1989) proposed the engagement of the left and right hemisphere to process the categorial relations and spatial co-ordinates of the stimuli (Kosslyn, 1987).

EEG power analysis of the alpha frequency band showed a reduction over the left hemi-
sphere during verbal or mathematical performances, and over the right hemisphere during spatial tasks (Morgan et al., 1971; Galin and Ornstein, 1972; Butler and Glass, 1974). Haynes and Moore (1981) showed that females – in contrast to males – had lower alpha activity over the left hemisphere when they had to perform two verbal tasks. From this result the authors concluded that the left hemisphere in females was more involved during the tasks than the right hemisphere. Ray et al. (1981) studied EEG asymmetry for high and low spatial abilities in males and females. Males with high spatial abilities showed a relatively larger activity in the right hemisphere associated with successful performance. The opposite relationship was found in males with low spatial ability. No consistent patterns were found in both female groups. Despite these results another reason for the involvement of different brain areas may be different levels of task complexity. In a study by Ornstein et al. (1980) healthy people performed six spatial tasks and one verbal task. EEG was recorded bilaterally from central and parietal areas. In spatial tasks the right hemispheric involvement was stronger than during the verbal task. Only the mental rotation task was different insofar as the EEG patterns were similar to the verbal task and showed a high engagement of the left hemisphere. The authors concluded that subjects used analytical strategies to perform the mental rotation task. No sex differences were evaluated. Differences between both genders were shown in a study by Burgess and Gruzelier (1997). Healthy subjects had to perform recognition memory tasks of words and faces. Their results showed significant attenuation of alpha, beta1 and beta2 in the right tempororo-parietal region for faces but not significant changes for words. Only in females left temporal changes for the word task were found.

EEG coherence analysis yields hints on the functional coupling between different brain areas from where the signals are recorded and thus on the involvement of brain areas in processing mechanisms of cognitive tasks. Coherence values complement data obtained by power spectral analysis which does not give any information of functional relationships between two signals (Shaw et al., 1978). Mathematically, coherence may be considered as a correlation coefficient per frequency or frequency band (Shaw, 1984) and is obtained by normalising the cross-power spectrum. It is independent of the EEG amplitudes. Coherence may also be considered as a measure of phase or time lag stability between corresponding frequency components of two signals (Nunez et al., 1997).

Coherence analysis revealed gender differences in reading tasks (Petsche et al., 1987; Rescher, 1992), in tactile tests (Rescher, 1996; Rescher and Rappelsberger, 1995, 1996, 1997), during visual–spatial tasks (Kriegsteiner, 1985; Lacroix et al., 1993; Rescher, 1996), during photic stimulation (Nanbu et al., 1995) and at rest (Petsche et al., 1988; Rescher et al., 1998). As demonstrated by Corsi-Cabrera et al. (1997) intra- and interhemispheric coupling during spatial performance is influenced not only by sex but also in subjects with high and low spatial abilities.

Summing up, the involvement of the right and left hemisphere during cognitive performances depend on the task, on good or poor cognitive abilities in this specific task, on the used strategy, on the level of task difficulty, on sex and handiness of the subjects, and many other factors. Different methods are available to aid functional localisation (EEG, PET or fMRI) but an essential problem is the comparison of the results across these methods.

The aim of this study was to address sex differences in amplitude and coherence during a complex mental rotation task. With respect to anatomical differences in both sexes and depending on the possible interpretation of coherence as a measure of functional relationships between brain areas it is hypothesised that the interhemispheric coupling is stronger over the posterior regions in females. The paradigm was designed on the understanding that females and males show no differences in the performance of spatial tasks. Good and poor spatial abilities were not considered in this investigation. In spite of this, the intra- and interhemispheric changes in the cortical representation in both genders should be different.
2. Methods

2.1. Subjects and task

This study was conducted with 15 right-handed female and 15 right-handed male students. The age range in the two groups was 20–30 years (females: mean 24.5 years, S.D. 3.0, median 25 years; males: mean 24.0 years, S.D. 2.5, median 24). All subjects were given the Leistungsprüf- system (LPS) by Horn (1962). In this study, the IQ in females had a mean of 123.33 (S.D. 10.61) and the mean in males was 125.87 (S.D. 9.66). The raw data in the subtests for spatial abilities showed a mean of 117.80 (S.D. 23.0) in females and a mean of 126.8 (13.52) in males. T-test for equality of means were used and no significant difference was found.

The paradigm for assessing visual–spatial abilities was the mental rotation test by Shepard and Metzler (1971). Six pictures were presented in random order. On each picture a pair of three-dimensional figures was shown at different orientations. Three pairs included identical figures and three were different. All subjects were asked to look at each pair and after mental rotation they had to decide whether the figures were identical or the mirror image. After 20 s they were asked to respond by saying ‘yes’ or ‘no’. Twenty seconds were chosen for presentation since extensive pre-tests without EEG recording revealed that subjects need approximately that time to solve the task. Standard deviation was only a few seconds. On average the number of correct answers during the EEG recording was approximately 50%. This number did not differ from the percentage during the pre-test and does not differ from answers by chance. However, after extensive discussions with the subjects following the test it must be assumed that the performance did not reach values far above 50% due to the difficulty of the task and not due to chance answers. Furthermore, no differences in the correct answers were found between males and females.

2.2. Electrophysiological methods

After carefully measuring and marking the standard positions (Fp1, Fp2, F7, F3, Fz, F4, F8, T6, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, O1, O2) according to the international 10/20 system, 19 gold electrodes were attached to the scalp. Reference electrodes were applied to both earlobes. EEG recordings were made against the mathematically averaged signals of both ear electrodes ([A1 + A2]/2; TC 0.3 s, Filter 35 Hz) according to the recommendation of Essl and Rappelsberger (1998). EEG was displayed on paper with a conventional Nihon Kohden 21 channel EEG recorder. The output of the EEG machine was connected to a Walter Graphek data acquisition system (sampling rate 128/s) to store the data on hard disk for off-line processing.

The experiments were conducted under consistent conditions. Only the experimenters and the subject were in the sound-attenuated recording room. Constant background noise was presented due to the equipment. Each subject was seated comfortably in an arm chair. Before and after the task condition the subjects were allowed to move. Eye movements were monitored with a movement sensor attached to one eyelid. The signals of the sensor were recorded on a separate channel.

EEG was recorded during the mental rotation task (six pictures each presented up to 20 s). In addition, control records with eyes opened were recorded before and after the task lasting approximately 1.5 min each. No significant differences between the EEG parameters of the two control records were found. Therefore, the control records were merged for the computation of baseline parameters. Amplitude and coherence changes during mental rotation were evaluated with respect to the corresponding baseline parameters.

 Artefacts were eliminated from further computation by visual inspection. As many as possible artefact free 2-s epochs were chosen for further processing. In females, between 17 and 56 epochs (median 35) and in males between 15 and 50 (median 33) were obtained for the task records. For the control records the number of epochs was 33–77 (median 55) in females and 23–66 (median 51) in males. Each epoch was Fourier transformed, and averaged power and cross-power spectra with a frequency resolution of 0.5 Hz.
were computed (absolute spectra). Power spectra (19) and cross-power spectra between all electrode pairs (171) were obtained for each record, i.e. mental rotation and control. Data reduction of the spectra was performed for five frequency bands: theta (4.0–7.5 Hz), alpha1 (8.0–10.0 Hz), alpha2 (10.5–12.5 Hz), beta1 (13.0–18.0 Hz), beta2 (18.5–24.0 Hz).

2.3. Statistical evaluation

For the evaluation of changes during the mental rotation task with respect to the baseline parameters, paired Wilcoxon tests were applied. Furthermore, to test whether the changes during the mental rotation test with respect to the baseline are different in females and males a direct test of significance between genders was adopted (Wilcoxon test of independent samples). The obtained rank sums were converted to error probabilities (IBM-Scientific Subroutine Package, 1970) and presented in ‘probability maps’. Fig. 1 shows the error probability maps of amplitude and coherence changes (mental rotation task vs. control) for five frequency bands (left column: females, middle column: males). The right column shows the error probability maps as a result to testing changes in females against changes in males evaluated by Wilcoxon test for independent samples.

The possible statistical analysis include multivariate parametric methods or N-fold univariate parametric or non-parametric tests. However, multivariate methods, in general, are not applicable because of the high-dimensionality on the one hand, and the comparatively small number of subjects on the other hand. In addition, with respect to multivariate analysis of variance, one generally faces the problem of lack of underlying unimodal, symmetrical distributions and of homogeneity of variance matrices. On the other hand, multivariate non-parametric methods do not exist for complex data structures as presented in this study.

In this paper, the results of N-fold univariate comparisons using Wilcoxon tests for the evaluation of differences between chosen parameters should only be considered as a descriptive data analysis. In the statistical sense, N-fold univariate comparisons lead to the problem of α-inflation if the individual significance levels are not adjusted. However, α-adjustments in the confirmatory sense for large N lead to unbearable high probabilities for not rejecting false null hypothesis. Therefore, the results should only be considered as a descriptive approach to yield hints at those of the multiple comparisons for which possible differences between two conditions exist. This approach can also be considered as a statistical filtering to indicate those differences which differ clearly from changes by chance. Therefore, in the following the term ‘significant’ is used only for the description but not for statistical confirmation of differences.

3. Results

Fig. 1 demonstrates changes in amplitude and coherence during mental rotation vs. control in females (left column), in males (middle column) and depicts differences of the changes between both genders (right column). In the theta band amplitude increased during mental rotation only in O1 (full circle) in the female group and in O1, O2, Pz and T6 in males. In alpha1,2 and beta1,2 amplitude decreased in both groups over widespread areas. No differences of amplitude changes were found between both genders.

In the theta band coherence increased between temporo-parietal-occipital electrodes in both groups. In the male group frontal electrodes were also involved in coherence increase. Concerning coherence decrease, in theta band decrease between T4 and other electrodes were more pronounced in females than in males. In contrast to this, coherence decrease between T3 and other sites were more pronounced in males. However, comparing the changes of both genders differences were found only between O1 and O2 and frontally (Fig. 1, right column, Table 2).

In alpha1, Fig. 1 (middle column) demonstrates that in males coherence increased mainly between
Fig. 1. Error probability maps of amplitude- and coherence changes (mental rotation task vs. control) according to paired Wilcoxon tests for five frequency bands (left column: females; middle column: males). Significant increase of amplitude is indicated by black circles and decrease by white circles. Grey shaded circles indicate no significant changes. Significant coherence increase is indicated by full lines and decrease by broken lines between pairs of electrodes. The right column shows the error probability maps as a result of testing changes in females against changes in males (Wilcoxon test for independent samples).
Table 1
Mean intrahemispherical changes during the mental rotation task vs. baseline in females and males*

<table>
<thead>
<tr>
<th>Intrahemispheric coherence</th>
<th>Theta</th>
<th>Alpha1</th>
<th>Alpha2</th>
<th>Beta1</th>
<th>Beta2</th>
</tr>
</thead>
<tbody>
<tr>
<td>C3–Cz</td>
<td>0.00 0.10</td>
<td>–0.10**</td>
<td>–0.02 0.01</td>
<td>–0.02**</td>
<td></td>
</tr>
<tr>
<td>T5–O1</td>
<td>0.06 0.00</td>
<td>0.06**</td>
<td>–0.07 0.04</td>
<td>–0.11**</td>
<td></td>
</tr>
<tr>
<td>C3–P3</td>
<td>0.13 0.01</td>
<td>–0.13**</td>
<td>–0.04 0.01</td>
<td>–0.05**</td>
<td></td>
</tr>
<tr>
<td>Fp1–T3</td>
<td>0.02 0.17</td>
<td>–0.15**</td>
<td>–0.03 0.02</td>
<td>–0.05**</td>
<td></td>
</tr>
<tr>
<td>Fz–T3</td>
<td>–0.17 –0.05</td>
<td>–0.13**</td>
<td>0.02 0.05</td>
<td>0.07**</td>
<td></td>
</tr>
<tr>
<td>T4–P4</td>
<td>0.01 0.04</td>
<td>0.05**</td>
<td>0.06 0.00</td>
<td>0.06***</td>
<td></td>
</tr>
<tr>
<td>T4–O2</td>
<td>0.06 0.01</td>
<td>0.02**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C3–T5</td>
<td>–0.01 –0.12</td>
<td>0.013**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cz–T5</td>
<td>0.03 0.01</td>
<td>0.02**</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Only those values are listed which were found to be significantly different in females and males according to the Wilcoxon test for independent samples (*P < 0.05; **P < 0.02; ***P < 0.01).
In females, increase was only found between O1 and O2, whereas O1 show decreased coherence with respect to several other electrodes. In the right column coherence changes between C3 and other sites are indicated as different between both genders. According to Table 2 and concerning the interplay between the two hemispheres, males showed considerable increase in C3–F4 and C3–C4, whereas females showed slight decrease. Intrahemispherically (Table 1) C3–Fz and C3–Cz increased in males whereas in females coherence changes were negligible. Yet, the opposite behaviour was observed in C3–P3: at this site females showed coherence increase whereas, males did not.

In alpha2 only in the female group (Fig. 1, left column) three connections of increased coherence extended from T4. In males coherence increase was observed between numerous positions with an imbalance in favour of T3. Coherence decrease in males concerned mainly electrode O1 and other sites in the left posterior region (Fig. 1, middle column). According to Table 2 males showed higher interhemispheric coherence increase in C3–C4. In contrast to this, coherence decreased in males but increased in females between T6 and O1 (Table 2). Intrahemispherically, both genders showed a decrease between C3 and T5, larger in males than in females (Table 1).

In beta1 coherence increase was found in both groups between T6 and other positions with, however, different topographical representations. In females increase occurred also between both occipital electrodes. Decrease was most pronounced between frontal and central electrodes in females. As for significant differences between both genders, most worth mentioning are the coherence changes between frontal electrodes and fronto-centro-temporal electrodes on the left hemisphere (Fig. 1, right column). Concerning interhemispheric coherence changes, in females generally coherence decreased whereas in males hardly any changes were observed (Table 2).

In beta2 the patterns of coherence changes in both genders were similar but different with respect to the other frequency bands. In both genders coherence increase prevailed between fronto-parietally, fronto-occipitally and temporal electrodes (Fig. 1, left and middle columns). As the right column demonstrates there are gender dependent differences on both tempo-parietal regions. Table 1 clearly shows that these differences are due to different changes of coherence: in the left hemisphere, females produce higher coherence increase between T5–C3 and T5–Cz than males. In the right hemisphere females produce increase during the test between T4–P4 and T4–O2, whereas males show clear decrease in coherence (Fig. 1, right column; Table 1.).

### Table 2

Mean interhemispherical changes during the mental rotation task vs. baseline in females and males

<table>
<thead>
<tr>
<th></th>
<th>Theta</th>
<th>Alpha1</th>
<th>Alpha2</th>
<th>Beta1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fp1–Fp2</td>
<td>–0.26</td>
<td>–0.05</td>
<td>–0.20**</td>
<td>–0.14</td>
</tr>
<tr>
<td>Fp1–F4</td>
<td>–0.29</td>
<td>–0.08</td>
<td>–0.21**</td>
<td>–0.09</td>
</tr>
<tr>
<td>Fp2–F3</td>
<td>–0.23</td>
<td>–0.04</td>
<td>–0.20**</td>
<td>–0.04</td>
</tr>
<tr>
<td>Fp2–C3</td>
<td></td>
<td></td>
<td></td>
<td>–0.07</td>
</tr>
<tr>
<td>Fp2–T3</td>
<td>–0.01</td>
<td>0.13</td>
<td>–0.14**</td>
<td>0.04</td>
</tr>
<tr>
<td>T6–O1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C3–C4</td>
<td>–0.04</td>
<td>0.08</td>
<td>–0.12**</td>
<td>–0.06</td>
</tr>
<tr>
<td>O1–O2</td>
<td>–0.04</td>
<td>0.00</td>
<td>–0.04**</td>
<td>–0.04</td>
</tr>
</tbody>
</table>

*Only those values are listed which were found to be significantly different in females and males according to the Wilcoxon test for independent samples (*P < 0.05; **P < 0.02; ***P < 0.01).
4. Discussion

EEG coherence, mainly interpreted as a measure for functional relationship between brain areas is largely influenced by the recording technique. Essl and Rappelsberger (1998) reported about the influence of the recording technique, i.e. the reference signal on coherence. Nunez et al. (1997) demonstrated the influence of different spatial scales on coherence and emphasised that conventional reference, average reference, bipolar and Laplacian yield partly independent measures of neocortical dynamic function. According to these examinations and based on the experiences and systematic investigations in our laboratory (Essl and Rappelsberger, 1998) in this study EEG was recorded against averaged signals picked up from both ear lobes. In this context it must be mentioned that this is different from recording against linked ears. Averaged ear recording means that a mathematical average of both ear lobe signals is used as reference, linked ear recording means a simple short circuit of both ear lobe electrodes.

Concerning the applied statistics, the non-parametric Wilcoxon statistics used in the EEG analysis needs no requirement concerning data structure, distribution, etc. as in parametric statistics. However, statistical tests of many variables, such as five frequency bands over 19 electrode positions with 171 coherence values poses the problem of the Type I error due to the inflation of the \(\alpha\)-value (Abt, 1983). This can be corrected according to Bonferroni. However, due to the large number of tests the error probability for rejecting the null hypothesis becomes unbearable low. Therefore, the chosen approach should be considered as a statistical filter technique to indicate those changes which differ clearly from changes by chance and usage of the term 'significant' is only for the description but not for statistical confirmation of differences.

Concerning amplitude changes during mental rotation, increase was found only in the theta band in both groups occipitally and parietally. The amplitude increase in theta most probably may be due to Lambda activity which frequently is observed in subjects looking at patterns (Zschocke, 1995). In our special case the patterns consisted of the three-dimensional figures. In all other electrode positions and frequency ranges amplitude decrease was observed in both groups indicating EEG desynchronisation. No significant differences of amplitude changes in both groups were found.

Coherence increase was observed in theta, beta1 and beta2 in the temporo-parietal and temporo-occipital electrodes in both groups. This indicates that the temporo-parietal and temporo-occipital visual association areas are involved during mental rotation. Kosslyn et al. (1993) suggested that mental images may be generated by activation of long-term visual memory. In a PET study they found an activation in the medial occipital lobe during visual mental imagery. In fMRI studies Roland and Gulyas (1994) reported that visual imagery does not require activation of the primary visual cortex. Our results, based on coherence increase in theta, beta1 and beta2 in posterior regions, support the involvement of visual association areas. Furthermore, in these three frequency bands coherence increased between O1 and O2 in females (Fig. 1, left column), whereas this was observed in males only in theta (Fig. 1, middle column). According to the descriptive Wilcoxon statistic of independent samples in theta increase of coherence during mental rotation is larger in females than in males (Fig. 1, right column, Table 2). The coupling between both occipital lobes in theta seems to be stronger in females than in males and may reflect a more intensive information transfer between both hemispheres in females than in males.

Generally, in theta, beta1 and beta2 coherence increase over the rear parts was found more symmetrical in females than in males. This can be interpreted by the more bilateral organisation of the females’ brain (McGlone, 1980; Bryden, 1989; Springer and Deutsch, 1989). According to the anatomical gender differences of the corpus callosum the transfer of information between both hemispheres seems to be more intensive in females (deLacoste-Utamsing and Holloway, 1982; Kimura, 1987; Adler, 1989; Witelson, 1989).
Coherence increase as a measure of callosal transfer in the intact brain was described by Montplaisir et al. (1990).

In contrast, to the findings described above a more bilateral involvement in males than in females could be found in both alpha bands. In alpha1 and alpha2 coherence increased between fronto-centro-parietal electrodes only in the male group (Fig. 1, middle column). The bilateral involvement of fronto-centro-parietal regions may reflect a more pronounced involvement in males than in females during mental rotation processing. The differences between females and males due to the engagement of both hemispheres seem to be related to the prevailing frequency band.

In addition to these results two important laterisation effects were found. First, in theta in the male group but not in females, a left-hemispheric coherence increase was found between fronto-central, fronto-temporal and centro-parietal electrodes (Fig. 1, middle column). According to the findings by Cooper and Shepard (1978) during this mental rotation task three distinct and successive processes can be distinguished: (1) the search for corresponding ends of both objects; (2) the rotation of the objects per se; and (3) the decision whether or not both objects are identically. Kosslyn (1987) postulated distinct subsystems during spatial abilities in both hemispheres. The left hemisphere seems to be more effective at assigning a spatial relation to a category, whereas the right one is more important at representing locations using a metric co-ordinate scheme. Moreover, the functions of ‘mental imagery’ decompose into numerous subabilities which appear to be differently lateralised (Kosslyn, 1987; Van Strien and Bouma, 1990). In addition, the function of each hemisphere during spatial processes were also investigated in clinical studies (Kosslyn et al., 1985; Corballis and Sergent, 1988, 1992; Alivisatos, 1992). All these processes may reflect the engagement of both hemispheres during complex tasks.

The left sided lateralisation effect in theta only in males including frontal, central temporal and parietal positions seems to be confirmed by a further investigation under equal conditions (actually unpublished). Theta frequency yield hints to be responsible for memory processes (Klimesch et al., 1994; Sarnthein et al., 1998). Thus, the idea takes place that the involvement of the left hemisphere could be responsible for additional memory processes, which were necessary to solve the problem in an efficient way. It is likely that coherence increase in the left hemisphere does not reflect rotational transformation itself but additional processes, which were engaged during problem solving. Consequently, this left-sided involvement could refer to additional memory processes combined with the usage of subsystems which were more important for problem solving in males than in females. It could be supposed that this difference between genders is related to the way in which females and males solve the problem. Moreover, no differences between both genders were found during test performance. Thus, this effect could not be related to a better performance in males (see above). However, up to now the meaning of theta frequency during memory processing and the involvement of distinct subsystems due to the differences in males and females are discussed.

In both genders a second lateralisation effect was found in beta1 in the right hemisphere (Beaumont et al., 1978), whereby the area below electrode T6 seems to play an important role during mental rotation. Farah (1989) reported that mental rotation depends primarily on structures in the posterior parts of the right hemisphere. Especially, beta frequency was found to play an important role in processing of higher cognitive functions (Rescher, 1992, 1996; Rescher and Rappelsberger, 1996; Petsche and Etlinger, 1998). Our results seem to confirm the findings described above, at least in beta1 frequency band. From our point of view the right hemispheric asymmetry could represent the process of rotational transformation itself in females and males. On one hand this idea was supported by the right hemispheric involvement and on the other hand on the occurrence in a higher frequency band (beta1) which seemed to be responsible for higher cognitive functions. Further studies of our group under the equivalent conditions showed the same
effect in beta1. Up to now this could be confirmed only for males because this study is not finished yet and consequently unpublished.

In addition, the greater asymmetry of coherence changes in males support the idea that the specialisation of the right hemisphere for spatial functions is greater in men than in women. This is consistent with clinical findings (McGlone and Kertesz, 1973).

Coherence decrease between F3, Fz, F4 in both groups and almost all frequency bands may reflect dissociation between functional processing units in frontal areas. Larger parts of the frontal lobes contribute to working memory and receive information from many other brain regions (Petrides, 1993). Frontal areas are loosely connected within the frontal regions but tightly connected with even distant parts of the brain which is supported by neuroanatomical studies (Goldman-Rakic, 1988). Thatcher et al. (1986) suggest in their two-compartment model that the frontal coherence pattern may be strongly influenced by distant fibre connections. This idea is supported by this and other coherence studies of our group (Petsche et al., 1987; Rescher, 1996; Rescher and Rappelsberger, 1996).

Sarnthein et al. (1998) found evidence that the interaction between prefrontal cortex and posterior association areas were responsible for working memory processes. Similar patterns of coherence increase in theta were found during two different tasks. During retention of character strings (verbal components of working memory) and retention of abstract line drawings (visuo-spatial components of working memory) prefrontal involvement was found bilaterally but more connections involving the right prefrontal cortex than the left. The authors suggested that — in contrast to all other frequency bands — the significant coherence increase in theta (4–7 Hz) between long distant regions mediate working memory processes.

In theta band, in both genders no significant changes between fronto-polar and frontal positions were observed. However, in females larger intra- and interhemispheric decrease of coherence was found between these electrodes than in males (Tables 1 and 2). In agreement with this finding, coherence decrease was also more pronounced in these areas in females than in males during tactile and reading tasks (Rescher, 1992; Rescher and Rappelsberger, 1996). This seems to be gender-specific for various cognitive functions.

Additional gender differences in the theta band concern the temporal electrodes. In females, decrease was found between electrode T4 and various other positions, whereas in males both temporal electrodes were involved but coherence decrease was found more pronounced between T3 and other positions than between T4 and other sites (Fig. 1, left and middle columns). However, as demonstrated in the right column of Fig. 1 no gender differences were found. Coherence decrease may be interpreted by a functional decoupling between both corresponding electrode sites. This may be a direct decoupling via cortico-cortical pathways probably due to more local information processing or may be caused by subcortical structures (Petsche and Etlinger, 1998). During spatial processing the hippocampus may play an important part in encoding new information. Early clinical studies postulate the importance of the temporal lobes and closely associated structures of the limbic system for learning and memory processing. Milner (1966) found evidence that the hippocampus and associated structures play an important role during the transition from short-term to long-term memory. Klimesch et al. (1994) postulate the necessity of the theta band for memory processing.

In alpha1 in females and in alpha2 in males coherence between O1 and other positions is decreased during the task with respect to the EEG at rest (Fig. 1, left and middle column). This may be due to more local information processing in the left visual areas in the alpha range (Petsche and Etlinger, 1998). Up to now there is no explanation for this isolated finding in the left occipital region.

Gender differences were found also in the beta1 band. In females, coherence decreased fronto-centrally and fronto-temporally in both hemispheres, whereas males showed almost no changes (Fig. 1 left and middle columns, Tables 1 and 2). Thus, the anterior parts of the left hemisphere
seem to have a more specialised function during mental rotation in females than in males. Our studies in right-handed females and males resulted in four main findings: (1) The assumption for unilateral specialisation mainly in the right hemisphere during mental rotation cannot be supported. Coherence changes demonstrate the involvement of bilateral and unilateral brain areas depending on the prevailing frequency band and genders, respectively. Furthermore, local processes (coherence decrease) as well as intensive co-operation between cortical areas (coherence increase) in females and males seems to be independent of the degree of mental rotation abilities. The differences especially in theta (left hemisphere) could rather depend on the way in which men and women perform the task. (2) Left sided coherence decrease in the beta1 band in females but not in males hint at a more specific role of the left temporal and frontal parts in females than in males during mental rotation, possibly caused by additional subcortical influences. (3) Coherence increase in beta1 in both groups show a trend for a right-sided lateralisation. This may indicate the importance of the right hemisphere for higher spatial functions independent of gender. However, the left hemisphere is more engaged in females than in males. Therefore, for higher spatial processes the right hemisphere seems to be more specialised in men than in women. (4) In posterior regions, females show rather symmetrical coherence increase in theta, beta1 and beta2. This may support the idea that the interhemispheric transfer is stronger in females than in males.

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