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EEG coherence during mental rotation of letters, hands and scenes

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ABSTRACT

The purpose of the present study was to investigate differences in the electrocortical synchronization pattern during mental rotation of three different object categories as well as six different rotation angles. Therefore, event-related coherence of the electroencephalographic (EEG) activity between selective frontal and parietal electrode pairs of ten subjects was measured during the performance of a mental rotation task consisting of rotation of letters, hands and scenes. Statistical analysis showed an increased coherence of frontal and parietal electrode pairs for the condition LETTER in comparison to the other conditions in the alpha$_1$- (8.5–10 Hz) and alpha$_2$-band (10, 5–12 Hz) supporting the notion of different mental rotation mechanisms for externally and internally represented objects. Additionally decreased coherence of the frontal and parietal electrode pairs was found for the rotation angles 30° to 150° in comparison to the 0° and 180° rotations for the alpha$_1$- and alpha$_2$-band as well as the gamma frequency band (30–45 Hz). It is assumed that this decrease of synchronization reflects the mental rotation process implying that the mental rotation process of 180° differs from the rotation process of all other rotation angles.

1. Introduction

Mental rotation implies the judgment of objects, which are presented in different orientations. Behavioral studies revealed that with growing disparity between the normal upright and the presented position of object reaction time increases (Ionta et al., 2007; Kessler and Thomson, 2010; Shepard and Metzler, 1971). This phenomenon was shown for different kinds of objects such as letters, human shapes (hands, body parts) and complex scenes (landscapes, table scenes). However, the interpretation of this phenomenon differs depending on object style. It has been suggested that external objects, such as letters, were mentally rotated in an allocentric reference frame before judging them (object-based transformation). On the contrary, for scenes and human shapes, instead of rotating the object a mental self-rotation is performed before defining it in an egocentric reference frame (egocentric perspective-taking) (Kessler and Thomson, 2010; Kozhevnikov and Hegarty, 2001; Zacks and Michelon, 2005). Behavioral experiments show that scene rotation is executed faster and more accurately than object rotation (Amorim and Stucchi, 1997; Keehner et al., 2006; Wraga et al., 1999; Zacks and Michelon, 2005); Furthermore hand rotation is faster and more accurately than object rotation (Kosslyn et al., 1998). However, only two of three stimulus categories have been considered in these studies. In order to close this research gap Dalecki et al. (2012) have been the first to compare all three stimulus categories within one experiment. The results confirmed the existence of distinct mechanisms for external stimuli based on object transformation and stimuli, such as scenes and body parts, based on an egocentric perspective-taking.

In addition to the behavioral evidence, neuroimaging studies investigating mental rotation have provided different electrocortical activation patterns for different object categories. However, differences could not clearly be reduced to the distinct object categories but rather differed within the object categories when investigated by different studies. Regarding mental rotation of external objects, one study reported activation of the left parietal cortex and the right caudate head (Alivisatos and Petrides, 1997). Another study found activation of the left and right parietal cortices and the associative visual cortex (Brodmann area (BA) 19) (Kosslyn et al., 1998), and again others determined activation of the right parietal cortex only (Harris et al., 2000; Núñez-Peña and Aznar-Casanova, 2009; Zacks et al., 2003). In a few studies mental rotation of hands was associated with activation of the left primary motor and insular cortices and BA 6, 7, and 9, (Kosslyn et al., 1998; Parsons et al., 1995) and in another study with activation of both parietal, extrastriate and premotor cortices (Vingerhoets et al., 2002). For mental rotation of scenes, Creem et al. (2001) found activation of the left posterior parietal, secondary visual, premotor and frontal areas, whereas Zacks et al. (2003) reported activation of the left temporal areas.

These various results indicate that mental rotation is a complex cognitive function involving numerous sub-processes located in different brain areas. But they cannot clearly support the existence of different mechanisms for mental rotation. However, studies using

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an electroencephalograph (EEG) found consistent results investigating event-related potentials (ERPs) during mental rotation for the different object categories (Heil, 2002; Jansen-Osmann and Heil, 2007; Milivojevic et al., 2009; Tao et al., 2009; Wijers et al., 1989). They found that ERPs over the parietal electrodes become more negative with increasing rotation angles, which is termed as rotation related negativity. A further EEG study focused on the synchronization pattern of mental rotation of external objects (Bhattacharya et al., 2001). Results showed increased synchronization between frontal cortex and parietal cortex in the gamma-band compared with resting condition. Indeed, this study provides a first insight in the communication of different brain regions during mental rotation, but it did not consider different object categories.

The purpose of the present study is to investigate the synchronization patterns during mental rotation of different object categories. Therefore, an approach similar to Bhattacharya et al. (2001) is used and combined with the approach of Dalecki et al. (2012), which contains three different object categories (LETTER, HAND and SCENE). In contrast to Bhattacharya et al. (2001), synchronization patterns are compared to 0° rotation rather than to a resting condition allowing to differentiate clearly between mental rotation processes and other task-involved cognitive performances such as the identification of the object alignment. Synchronization patterns are determined in the $alpha_1$- and $alpha_2$-band as well as in the gamma-band. Indeed, changes in synchronization during cognitive performances have been observed in different frequency bands (Gevins et al., 1997; Rodriguez et al., 1999; Sauseng et al., 2005; Varela, 1995; Singer and Gray, 1995; Weiss and Rappelsberger, 2000). Especially gamma-band synchronization is associated with large-scale cognitive integration (Rodriguez et al., 1999; Singer and Gray, 1995; Varela, 1995) But also changes of synchronization in the alpha-band have been found during several cognitive demands such as executive processes (Sauseng et al., 2005; Weiss and Rappelsberger, 2000). Therefore, both, low frequencies (alpha-bands) and high frequencies (gamma-band) are taken into consideration for the present study. Based on the hypothesis that different mechanisms for external and internal object categories exist (Kessler and Thomson, 2010; Kozhevnikov and Hegarty, 2001; Zacks and Michelon, 2005), different synchronization patterns for the condition letter in comparison to hand and scene are expected. Additionally differences in synchronization pattern for the 0° rotation compared with rotated objects are assumed.

2. Methods

Ten right-handed subjects (6 males), aged 26.7 ± 4.9 years, participated in this study. All were free of sensorimotor dysfunctions except corrected vision, and none of them reported prior experience in sensorimotor research. Prior, all subjects signed an informed consent form approved by the institutional ethics committee. This study has been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.1. Mental rotation

Subjects participated in three different mental rotation conditions (LETTER, HAND, SCENE), which have already been used in a previous study (Dalecki et al., 2012). Participants were sitting at a distance of 50 cm in front of a flat-screen monitor, on which objects in different orientations were sequentially presented. The only difference to the previous study was the presentation of objects: in the present study 3D shapes instead of 2D shapes were used, which were presented in an oblique plane (65° above the horizontal) (see Fig. 1). In the condition LETTER a “G” or “R” was displayed (see Fig. 1A left). The subjects were asked to judge whether the letter was non-reversed or mirror-reversed. For the condition HAND subjects were instructed to decide if a right or a left hand is presented (see Fig. 1A middle). In the condition SCENE images of a person sitting on a round table with a flower and a weapon (gun or knife) lying in front of the person were displayed (see Fig. 1A right). The task was to judge whether the weapon was to the person's left or right side. The pictures were displayed on a white background within a black circular mask. The order of versions was balanced between subjects. In each condition objects were presented in the orientations 0°, ±30°, ±60°, ±90°, ±120°, ±150° and 180°, in which 0° denotes fingers pointing upward, letters normally oriented, and persons turning their back to the observer, respectively. In each condition 48 different stimuli were presented: twelve orientations of two different shapes (letters “G” and “R”, two different hands, gun or knife) in two versions (letters were normal and mirror-reversed, left or right hand, weapon to the left or to the right). The 48 stimuli of the three conditions were each presented twice in a randomized order with a short rest break of 10 to 20 s in between; Thus, the total number of presented stimuli was 96 for each condition.

The subjects were instructed to respond to each stimulus quickly and accurately by pressing a key with their right or left index finger. The right key represented a non-reversed letter, a right hand and a weapon on the right side, respectively, and the left key represented the reversed alternative. Each stimulus was displayed until subjects responded, and was followed by a randomly varying inter-trial interval of 0.5 to 1.0 s. The subjects were immediately informed about incorrect responses by a short acoustic signal.

For statistical analysis the reaction time (RT) between stimulus onset and key press was averaged across clockwise and counterclockwise orientation angles, across the two respective stimulus shapes of each condition (“G” and “R”, two different hands, gun or knife), and across repetitions. Similar to the former study (Dalecki et al., 2012) no statistical differences were found between counter- and clockwise stimulus orientations for each angle. Therefore, seven rotation angles for each condition representing the orientations 0°, 30°, 60° 90°, 120°, 150° and 180° were differentiated. Wrong submissions and responses with RT > 3 s (2%) were excluded from the RT analysis. ANOVA observing the factor sex yielded no differences such that this factor was not taken into consideration for further analyses ($p = 0.19$). RT data was submitted to an analysis of variance (ANOVA) with repeated measures on the within-factors Condition (LETTER, HAND, SCENE) and Rotation (0°, 30°, 60°, 90°, 120°, 150°, 180°). Significant effects were scrutinized by Fisher's LSD post-hoc tests.

2.2. EEG

During the whole experiment spontaneous EEG signals were recorded using 64 electrodes arranged according to the extended 10–20-system (Jasper, 1958) located in an elastic cap (ANT, WaveGuard Cap). Impedance was kept below 5 kΩ. Additionally, vertical eye blinks and horizontal eye movements were recorded by two EOG channels placed below and on the outer edge of the left (right) eye. Signals were digitalized by the Asa-Lab TM high density Cap-Amplifier (ANT, Enschede, Netherlands) with a sampling frequency of 1024 Hz and A/D precision of 22 bit. EEG signals were filtered offline (Brain Vision Analyzer software, Brain Products, Munich, Germany) with Butterworth zero phase filters including a notch-filter at 50 Hz, a low cutoff at 3 Hz and a high cutoff at 50 Hz with a time constant of 0.0531 s and 24 dB/oct. For further analysis 800 ms segments relative to the stimulus onset (0 to 800 ms) of the mental rotation task were used, while error segments were rejected. An ocular correction with an independent component analysis algorithm (Infomax Restricted) was implemented and a semiautomatic artifact correction algorithm allowing a maximum voltage step of 50 μV/ms and an amplitude range of −100 to 100 μV were executed. Identified artifacts were marked from 200 ms before and after the event and were manually removed. Afterwards data was visually inspected to eliminate further artifacts if needed. Following the baseline correction all segments were subdivided according to the 7 different rotation angles from 0° to 180°.

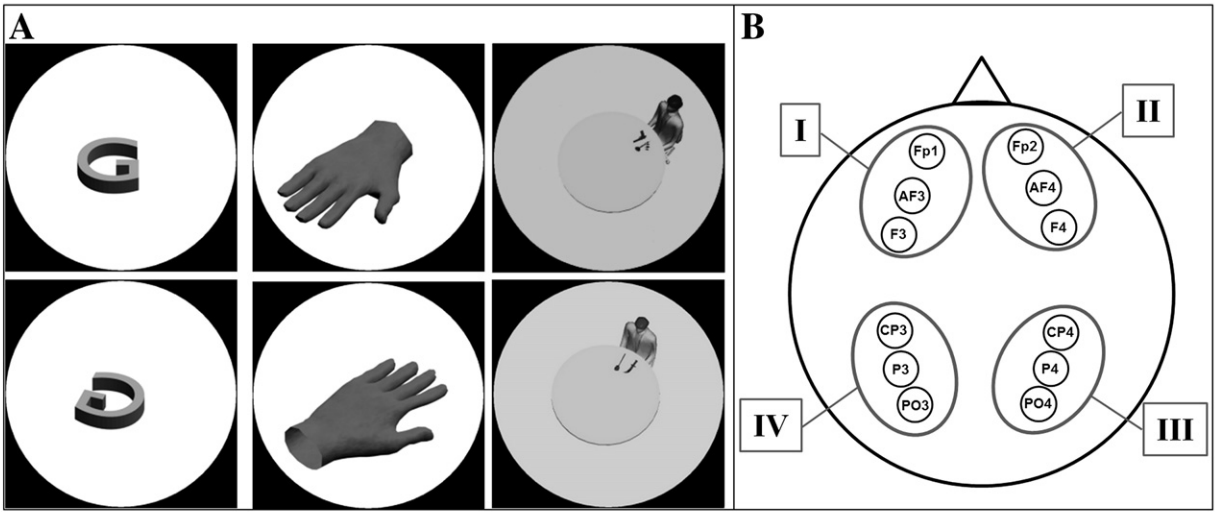

Fig. 1. A. Examples of stimuli of the conditions LETTER (left panel), HAND (mid panel) and SCENE (right panel). The top row represents stimuli requiring a right button press and the bottom row stimuli requiring a left button press. B. Position of the 12 electrodes which were used for coherence analysis. According to the different intrahemispheric (INTRA) and interhemispheric (INTER) networks electrode pairs were defined between or within the particular electrode groups I, II, III and IV: INTRA frontal within groups I and II, INTRA parietal within groups III and IV, INTRA fronto-parietal between groups I and IV and between groups II and III, INTER frontal between groups I and II, INTER parietal between groups III and IV and INTER fronto-parietal between groups I and III and between groups II and IV.

The signals were transformed in the frequency domain by using a Fast Fourier Transformation with a Hanning window function. Coherence was calculated as the quotient from cross-spectrum and auto-spectrum implemented in the Brain Vision Analyzer software (Brain Products, Munich, Germany):

$$Coh(c1,c2)(f) = |CS(c1,c2)(f)|^2/(|CS(c1,c1)(f)||CS(c2,c2)(f)|,$$

with $CS(c1, c2)(f) = \sum c1, i(f)\ c2, i(f)$ with fixed frequency f and fixed electrode c. Totaling is carried out using segment number i.

Selected electrodes located over the frontal and parietal cortices were included in the analyses (see Fig. 1B). Coherence values for each condition (LETTER, HAND, SCENE) and each rotation angle (0°–180°) were measured for each subject in three different frequency bands (alpha$_1$: 8.5–10 Hz; alpha$_2$: 10,5–12 Hz; gamma: 30–45 Hz). To differentiate between intra-hemispheric and inter-hemispheric as well as between frontal, parietal and fronto-parietal connections a method similar to that applied by Sauseng et al. (2005) was used. Therefore, the coherence values of the following electrode pairs, which were Fisher-Z transformed, were quantified.

1. For intra-hemispheric networks:
   a. Frontal: Fp1-AF3, Fp1-F3, AF3-F3, Fp2-AF4, Fp2-F4, AF4-F4
   b. Parietal: CP3-P3, CP3-PO3, P3-PO3, CP4-P4, CP4-PO4, P4-PO4
   c. Fronto-parietal: F3-P3, F3-PO3, AF3-P3, AF3-PO3, F4-P4, F4-PO4, AF4-P4, AF4-PO4.
2. For inter-hemispheric networks:
   a. Frontal: Fp1-Fp2, F3-F4, AF3-AF4, Fp1-F4, Fp1-AF4, F3-Fp2, F3-AF4, AF3-Fp2, AF3, F4
   b. Parietal: CP3-CP4, P3-P4, PO3-PO4, CP3-P4, CP3-PO4, P3-CP4, P3-PO4, PO3-CP4, PO3-P4
   c. Fronto-parietal: F3-P4, F3-PO4, P3-F4, P3-AF4, PO3-F4, PO3-AF4, AF3-P4, AF3-PO4.

Coherence values of electrode pairs representing one of the six defined networks (Fig. 1B) were averaged in order to get one value per network. Accordingly 126 coherence values were used for each frequency band: 3 conditions (LETTER, HAND, SCENE) × 7 Rotation angles (0°, 30°, 60°, 90°, 120°, 150°, 180°) × 6 networks (intra-hemispheric: frontal, parietal, fronto-parietal and inter-hemispheric: frontal, parietal, fronto-parietal). For statistical analyses we calculated one three-way ANOVA using the intra-hemispheric data and a second one using the inter-hemispheric data with repeated measures on the three factors Condition (LETTER, HAND, SCENE), Rotation (0°, 30°, 60°, 90°, 120°, 150°, 180°) and Network (frontal, parietal, fronto-parietal) for all three frequency bands.

Additionally, event-related power was calculated for the 800 ms segments for each condition and each rotation angle within the three frequency bands (alpha$_1$, alpha$_2$ and gamma). Power values for the frontal electrodes (FP1, FP2, AF3, AF4, F3, F4) and for the parietal electrodes (CP3, CP4, P3, P4, PO3, PO4) were averaged respectively. For statistical analyses a three-way ANOVA with repeated measures on the three factors Condition (LETTER, HAND, SCENE), Rotation (0°, 30°, 60°, 90°, 120°, 150°, 180°) and AREA (frontal, parietal) were calculated for all three frequency bands.

3. Results

3.1. Behavioral data

Fig. 2 illustrates that an increase of stimulus rotation from 0° to 180° led to an increase of RT for all three conditions, whereas reaction times of the condition LETTER were the slowest for the rotation angles 0° to 150° compared to the other conditions. Reaction times of the condition HAND were slower than for SCENE for all rotation angles and even slower than in the condition LETTER for the 180° rotation. ANOVA yielded significant effects for Condition ($F(2,44) = 6.26$, $p < 0.01$), Rotation ($F(6,132) = 83.45$, $p < 0.001$), and Condition ∗ Rotation ($F(12,264) = 4.94$, $p < 0.001$). For the factor Condition LSD post-hoc test showed that all three conditions differed significantly (all $p < 0.05$). LSD post-hoc test for Rotation resulted in significant differences between rotation angles above 60°. LSD post-hoc test of the interaction between Condition ∗ Rotation showed significant differences between the condition LETTER and the conditions HAND and SCENE for all rotation angles except for 150° between LETTER and HAND. The Conditions HAND and SCENE differed significantly for the rotation angles 120°–180° only.

3.2. EEG

Analysis of the factor Network showed that behavior of alpha$_1$- and alpha$_2$-bands was very similar but differed from gamma-band results. For the alpha-bands significant differences for the factors Condition,

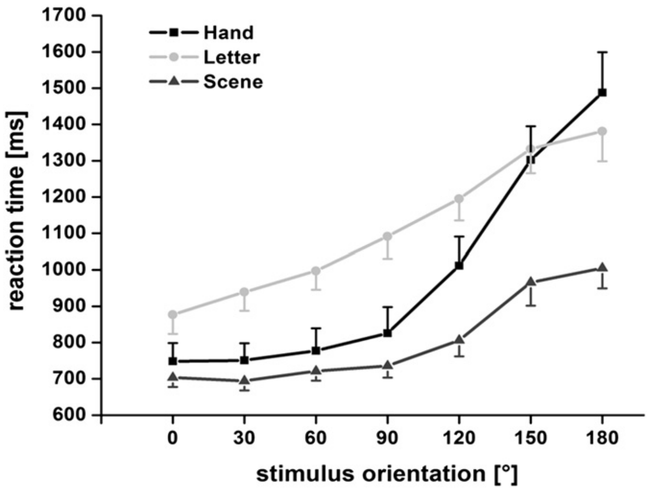

Fig. 2. Reaction times of correct responses. Symbols represent across—subject means and bars standard errors.

Rotation, Network and the interaction of Condition ∗ Rotation (except of the alpha$_2$-band of inter-hemispheric coherence) were found for both intra-hemispheric and inter-hemispheric network analyses (Table 1). LSD post-hoc tests for the factor Condition resulted in a significant greater coherence for the condition LETTER than for HAND and SCENE as well as for the intra-hemispheric and the inter-hemipheric networks in both alpha-bands (Fig. 3A). LSD post-hoc tests for the factor Rotation showed that for intra-hemispheric networks in alpha$_1$-band, the 0° rotation differs significantly from 30° to 120° rotation and the 180° rotation from 30° to 150° rotation; in alpha$_2$-band the 0° and 180° rotations differs significantly from 30° to 150° rotation. For inter-hemispheric networks, in both alpha-bands the 0° rotation differs significantly from 30° to 120° rotation and 180° rotation differs significantly from all other kinds of rotation (Fig. 3B).

LSD post-hoc test for the factor Network showed a significant greater coherence for the frontal network than for the parietal and the fronto-parietal networks for intra-hemispheric connections (Fig. 4A). For the inter-hemispheric connections LSD post-hoc test indicated that all three networks differed significantly in the alpha$_1$-band showing the highest coherence for the fronto-parietal network and the lowest for the parietal network (Fig. 4B). For alpha$_2$-band only the parietal network differed significantly from the others. LSD post-hoc test of the interaction of Condition ∗ Rotation confirmed the greatest coherence for the condition LETTER and the lowest for the condition SCENE most pronounced for the rotation angles 30°, 60°, 150° and 180°.

Additionally, regarding the alpha$_1$-band of intra-hemispheric network ANOVA a significant effect for the interaction of Rotation ∗ Network was observed. LSD post-hoc test revealed a significant greater coherence for the 0° rotation than for other rotation angles for all three networks.

For the gamma-band we found no significant effect for the factor Condition (Fig. 3A). For the intra-hemispheric connections ANOVA yielded a significant effect for the factors Rotation and Network and for the interaction of Condition ∗ Rotation. LSD post-hoc test for the factor rotation revealed a significant greater coherence for 0° and 180° rotations in comparison to the other rotation angles (Fig. 3B). LSD post-hoc test for the factor Network revealed a significant difference between all three networks with the greatest coherence in the parietal network and the lowest in the fronto-parietal network (Fig. 5A). Post-hoc test of the interaction of Condition ∗ Rotation showed that all three conditions differed significantly for the 180° rotation with the greatest coherence in the condition HAND and the lowest in the condition SCENE. For the inter-hemispheric connections ANOVA only resulted in a significant effect for the factor Rotation and the interaction of Condition ∗ Rotation. LSD-post-hoc test revealed similar results as for the intra-hemispheric connections.

Results of event-related power showed no significant effects in all three frequency bands, even though power values decrease from LETTER Condition to HAND and SCENE conditions for the alpha-bands (Fig. 6).

4. Discussion

The purpose of this study was to determine differences in electrocortical synchronization patterns for mental rotation of three different object categories as used in previous studies and for different rotation angles. Similar to the study of Dalecki et al. (2012) intra-individual data of subjects, each performing all three mental

Table 1
Statistical outcomes of ANOVAs of the coherence values.

		Intra-hemispheric connections	Inter-hemispheric connections
Alpha$_1$	Condition	$F(2,18) = 4.52^{*}$	$F(2,18) = 4.70^{*}$
	Rotation	$F(6,54) = 6.95^{***}$	$F(6,54) = 10.21^{***}$
	Network	$F(2,18) = 12.00^{***}$	$F(2,18) = 67.56^{***}$
	Condition ∗ Rotation	$F(12,108) = 2.67^{**}$	$F(12,108) = 2.95^{**}$
	Condition ∗ Network	$F(4,36) = 2.23^{n.s.}$	$F(4,36) = 1.99^{n.s.}$
	Rotation ∗ Network	$F(12,108) = 1.87^{*}$	$F(12,108) = 1.03^{n.s.}$
	Condition ∗ Rotation ∗ Network	$F(24,216) = 0.65^{n.s.}$	$F(24,216) = 1.52^{n.s.}$
Alpha$_2$	Condition	$F(2,18) = 5.00^{*}$	$F(2,18) = 4.18^{*}$
	Rotation	$F(6,54) = 11.13^{***}$	$F(6,54) = 9.25^{***}$
	Network	$F(2,18) = 14.32^{***}$	$F(2,18) = 30.83^{***}$
	Condition ∗ Rotation	$F(12,108) = 2.17^{*}$	$F(12,108) = 1.62^{n.s.}$
	Condition ∗ Network	$F(4,36) = 0.26^{n.s.}$	$F(4,36) = 1.13^{n.s.}$
	Rotation ∗ Network	$F(12,108) = 0.46^{n.s.}$	$F(12,108) = 0.91^{n.s.}$
	Condition ∗ Rotation ∗ Network	$F(24,216) = 1.10^{n.s.}$	$F(24,216) = 0.74^{n.s.}$
Gamma	Condition	$F(2,18) = 0.82^{n.s.}$	$F(2,18) = 2.26^{n.s.}$
	Rotation	$F(6,54) = 35.58^{***}$	$F(6,54) = 34.95^{***}$
	Network	$F(2,18) = 11.86^{***}$	$F(2,18) = 3.47^{n.s.}$
	Condition ∗ Rotation	$F(12,108) = 4.31^{***}$	$F(12,108) = 4.16^{***}$
	Condition ∗ Network	$F(4,36) = 1.25^{n.s.}$	$F(4,36) = 0.31^{n.s.}$
	Rotation ∗ Network	$F(12,108) = 1.09^{n.s.}$	$F(12,108) = 0.55^{n.s.}$
	Condition ∗ Rotation ∗ Network	$F(24,216) = 1.03^{n.s.}$	$F(24,216) = 0.88^{n.s.}$

$^{n.s.}$ $p > 0.05$.
*** $p \le 0.001$.
** $p \le 0.01$.
* $p \le 0.05$.

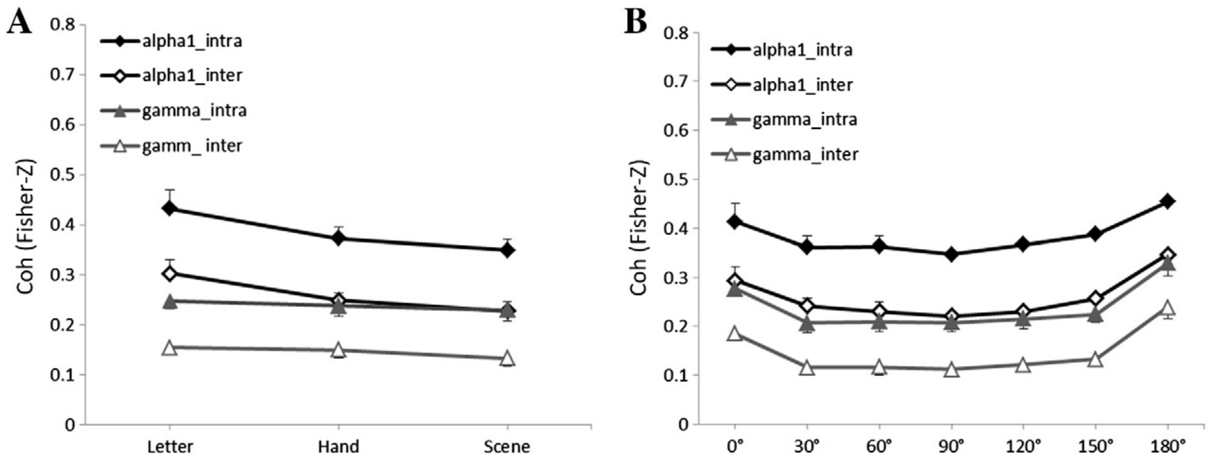

Fig. 3. A. Fisher-Z coherence for the conditions LETTER, HAND and SCENE averaged across all rotation angles and subjects separately for the intra-hemispheric and inter-hemispheric networks with bars representing standard errors. Depicted are the results of the gamma-band and the alpha$_1$-band, which data was comparable to the results of the alpha$_2$-band. B. Fisher-Z coherence for the seven different rotation angles (0°, 30°, 60°, 90°, 120°, 150°, 180°) averaged across all three conditions and subjects separately for the intra-hemispheric and inter-hemispheric networks with bars representing standard errors. Depicted are the results of the gamma-band and the alpha$_1$-band, which data was comparable to the results of the alpha$_2$-band.

rotation conditions (LETTER, HAND and SCENE), was compared. Behavioral data confirmed existing results showing that scene rotation was faster than object and hand rotations, while hand rotation was faster than object rotation (Amorim and Stucchi, 1997; Keehner et al., 2006; Kosslyn et al., 1998; Wraga et al., 1999; Zacks and Michelon, 2005).

EEG results showed a significant greater synchronization for the condition LETTER than for the conditions HAND and SCENE for the intra-hemispheric and the inter-hemispheric networks in both alpha bands. Regarding the gamma-band coherence did not differ between the conditions. These results support the existence of different rotation processes for letters compared with scenes and hands, which is manifested in the alpha-bands rather than in the gamma-band. Taking the proposed theory that letters are mentally rotated in an allocentric reference frame (Jola, 2005), whereas for the mental rotation of scenes and hands an egocentric reference frame is used (Kozhevnikov and

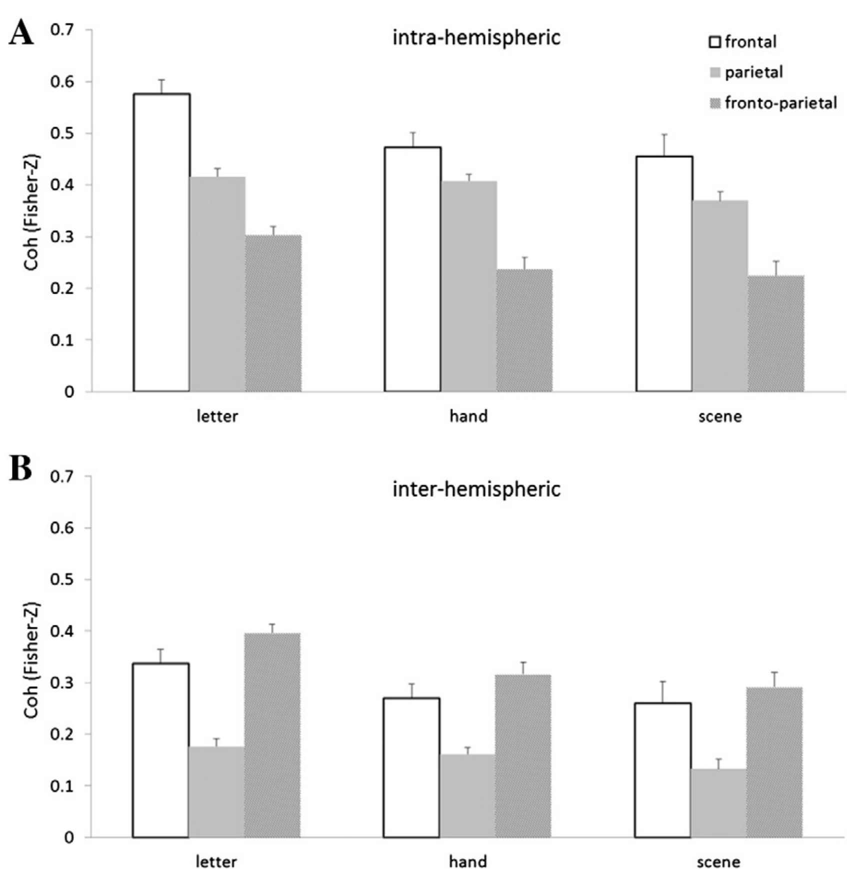

Fig. 4. Fisher-Z coherence as a function of condition (LETTER, HAND and SCENE) and Network (frontal, parietal, fronto-parietal) of the alpha$_1$-band, which results were similar to results of the alpha$_2$-band for A the intra-hemispheric networks and B the inter-hemispheric networks.

Hegarty, 2001; Kozhevnikov et al., 2006; Wraga et al., 1999), the allocentric object transformation is attended by higher synchronization in the alpha-bands than mental rotation processes based on an egocentric perspective-taking.

Furthermore, synchronization in the alpha-bands and in the gamma-band decreased from 0° to 30° and again increased significantly for 180° rotation. At first glance, this U-shaped course does not reflect the course of reaction times gradually increasing with larger rotation angles. It rather indicates a special role for the 180° rotation compared to the other rotation angles. Indeed, the 180° rotation matching a two-axes inversion has been described as a special parameter: mental rotation of 180° seems to involve distinct task-specific processes compared with mental rotation of smaller rotations (Dalecki et al., 2012; Franklin et al., 1992; Shelton and McNamara, 2001). Thus, the found synchronization pattern for the different rotation angles might reflect the different processes of mental rotation of 180° and smaller angles: the decrease of synchronization from 30° to 150° rotation might reflect the task-specific processes for mental rotation of these angles. In contrast, mental rotation processes of 180° are not accompanied by such a decrease of synchronization.

Indeed, the relation between the cognitive load of the different conditions and rotation angles, reflected by the reaction times, and the synchronization patterns seems inconsistent. Higher reaction times have been found for the LETTER condition than for the SCENE and HAND conditions which indicates a higher cognitive load. Therefore, a load-dependent increase of alpha-band synchronization can be postulated. In contrast, the mental rotation process of 30° to 150° angles is associated with a decrease of synchronization. However, a closer look reveals that mental rotation of letters is not necessarily a more demanding process than mental rotation of scenes and hands, but rather less demanding. Reaction times of LETTER condition compared to HAND and SCENE conditions were even greater without any rotation of the object (0° rotation). In particular, that means that the identification of the object alignment of letters, namely non-reversed versus mirror-reversed orientation, was more difficult than differentiating between right and left hand and the position of the weapon in front of the avatar. The fact that reaction times of HAND condition show a stronger increase with greater rotation angles converging against the reaction times of LETTER condition supports this assumption. On that basis, two interpretations can be suggested: I) if the increased synchronization in the alpha-band primary indicates the process of object discrimination, it will reflect a higher cognitive load; or II) if it is a sign of mental rotating process, it will reflect a decreased cognitive load. Indeed, several studies discussed that upper alpha oscillations can be modulated by memory load, but contradictory (Gevins et al., 1997; Jensen et al., 2002; Klimesch, 1999). Some found a load-dependent increase (Jensen et al., 2002; Klimesch, 1999; Krause et al., 2008), while others demonstrated a decrease of alpha power (Gevins et al., 1997). Sauseng et al. (2005) found a decrease of upper alpha coherence with executive demands. Hummel and Gerloff (2005) showed that larger interregional synchrony in the alpha band is associated with greater success in task performance. Due to the fact that in the present study a decrease of synchronization as well as an increase of synchronization of the alpha-bands is related to a higher cognitive load, we suggest, like Jensen et al. (2002), that activity in the alpha-band does not simply reflect general cognitive load but depends on the quality of the cognitive demand.

Additionally to the task-specific changes in alpha-band synchronization, a decrease of synchronization was also found for gamma-band synchronization in the course of the different rotation angles. As

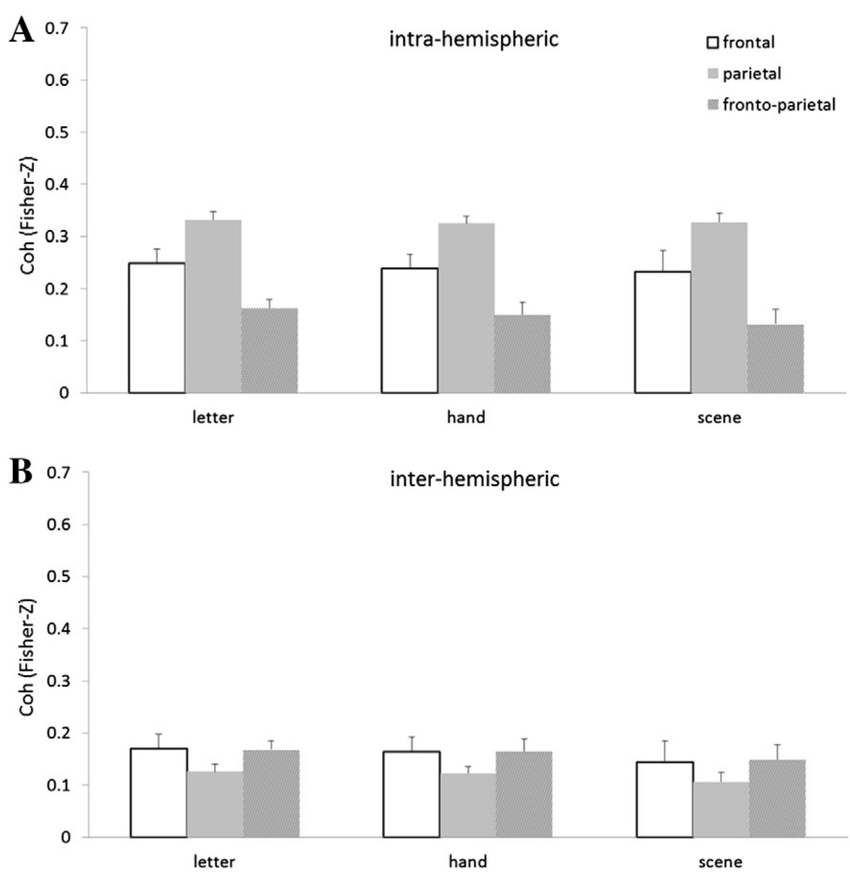

Fig. 5. Fisher-Z coherence as a function of condition (LETTER, HAND and SCENE) and network (frontal, parietal, fronto-parietal) of the gamma-band for A the intra-hemispheric networks and B the inter-hemispheric networks.

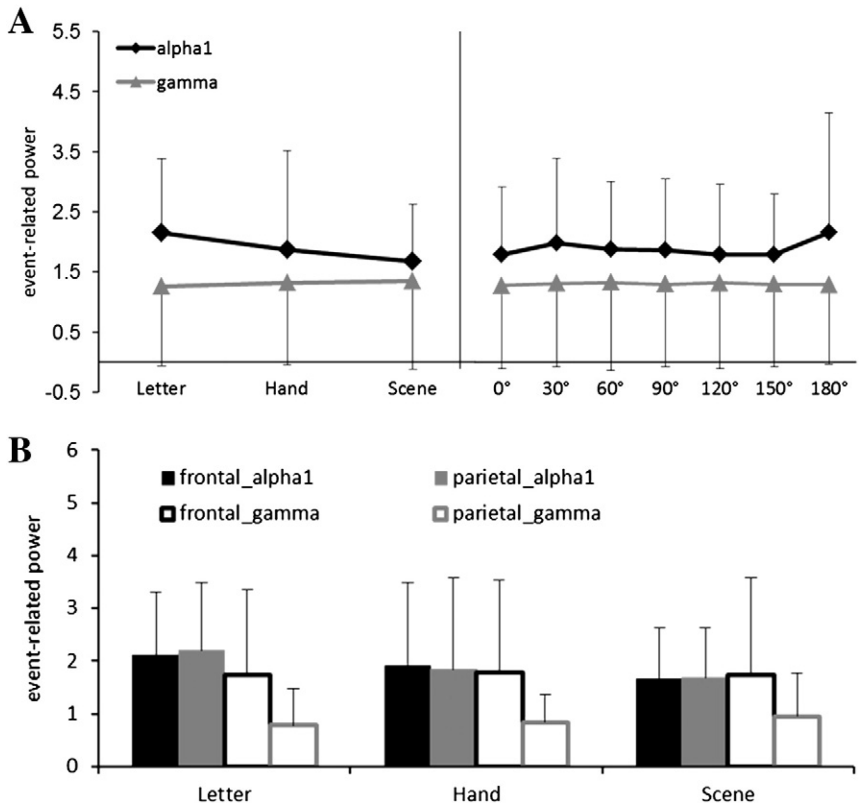

Fig. 6. Event-related power of the $alpha_1$-band (comparable to $alpha_2$-band) and the gamma band A for the conditions LETTER, HAND and SCENE averaged across all rotation angles and subjects (left panel) and for the seven different rotation angles (0°, 30°, 60°, 90°, 120°, 150°, 180°) averaged across all three conditions and subjects (right panel) and B as a function of condition (LETTER, HAND and SCENE) and area (frontal, parietal).

mentioned in the introduction, gamma-band coherence has been proposed as synchronization of widely distributed cell assemblies underlying a cognitive performance (Bhattacharya et al., 2001; Rodriguez et al., 1999; Singer and Gray, 1995; Varela, 1995). However, a few studies reported a decrease in gamma-band activity in relation to cognitive processing (Hirata et al., 2004; Lachaux et al., 2008). Rodriguez et al. (1999) observed an active desynchronization in the gamma-band during a visual perception task. They suggested that desynchronization in the gamma-band reflects an active decoupling of involved cell assemblies allowing to proceed from one cognitive act to another. In the case of mental rotation, this could be perception and rotation of the object.

As a further result we found no differences of coherence in the specified intra-hemispheric and inter-hemispheric networks between 0° and the other rotation angles. Therefore, the synchronization patterns of the different networks seem not to be explicitly attributed to the process of mental rotation but rather to other cognitive processes, which are involved in mental rotation tasks like inhibition or working memory processes. Regarding intra-hemispheric connections of the alpha-bands the highest synchronization was found between frontal electrodes and the lowest between fronto-parietal electrodes. A similar synchronization pattern in the alpha-bands was found by Sauseng et al. (2005) during a visuospatial working memory task, but it was not differentiated between intra-hemispheric and inter-hemispheric connections. For inter-hemispheric connections, we found higher coherence in the fronto-parietal and frontal networks than in the parietal network. Both networks were associated with executive functions and visuospatial working memory tasks (Collette et al., 1999; Kondo et al., 2004; Sauseng et al., 2005). For inter-hemispheric networks, coherence in total was lower than for intra-hemispheric connections in the frontal and parietal networks, which might be caused by longer ranges for inter-hemispheric connections. In contrast to the alpha-bands, intra-hemispheric connections in the gamma-band of the parietal electrodes showed the strongest synchronization compared with the frontal and the fronto-parietal connections.

In contrast to the described synchronization differences we found no significant event-related power changes in the alpha-bands and the gamma-band such that we can postulate that differences in coherence are not caused by oscillatory power changes, although coherence is affected by phase coupling and power changes.

Indeed, interpretations of the results are rather speculative since this is the first study comparing coherence of different conditions and the first study considering different rotation angles.

Due to several studies (e.g. Astur et al., 2004; Lawton, 2010) it has been established that mental rotation tasks produce one of the largest sex differences in cognition. This phenomenon has been attributed to social and educational factors, or to the use of different problem-solving strategies (Coluccia and Louse, 2004). However, like the present study, other studies reported no sex differences (Dalecki et al., 2012; Roberts and Bell, 2000). In the present study and as well in the study of Dalecki et al. (2012) subjects were young students with comparable social and educational background. Based on similar work and leisure activities they were comparably familiar with computer-based performance. Indeed, Roberts and Bell (2000) could show, that familiarization with computer performance suspends sex differences in a mental rotation task.

In conclusion, a decrease of synchronization for rotation angles of 30° to 150° and an increase for 180° was found for the alpha- and gamma-bands, which could be interpreted as a neural correlate of the mental rotation process, which is different for 180° and the smaller rotation angles. Additionally, our data supports the hypothesis of different mental rotation processes for externally versus internally represented objects shown by a higher synchronization during mental rotation of external objects, which only occurs in the alpha-bands.

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