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Age-related differences of neural connectivity during mental rotation

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ABSTRACT

The purpose of the present study was to investigate age-related effects on functional brain networks during a mental rotation task. At behavioral level age-related cognitive deficits have been shown. Cognitive deficits in older adults are associated with structural decline, especially in frontal and parietal areas and in the corpus callosum. In consequence, functional networks are affected by old age as well. To this end, a graph theoretical approach was taken, which quantifies the global and local efficiency as well as the cost efficiency of frontal and parietal intrahemispheric and interhemispheric networks. Main results indicate that intrahemispheric and interhemispheric networks are differently affected by older age: in the left frontal and the left and right parietal intrahemispheric networks global and local efficiency was reduced, whereas in frontal and parietal interhemispheric networks cost efficiency was decreased.

1. Introduction

Mental rotation tasks consider the ability of judging objects, which are presented in different orientations and were firstly introduced by Shepard and Metzler (1971). In this study subjects had to judge whether two objects which were presented are similar. They could show an increasing reaction time with growing angle disparity between both presented objects. Therefore, it has been suggested that during the mental rotation processing the presented stimuli were first mentally rotated into an equal position before a judgment was made. Further studies, using different kinds of objects, obtained similar results (Dalecki et al., 2012; Ionta et al., 2007; Kessler and Thomson, 2010; Thomas et al., 2013).

Objects can be classified into three categories: mental rotation of external objects (letters, cubes), of human shapes (hands, body parts) and of complex scenes (landscapes, table scenes). Depending on the object category mental rotation processes were interpreted in different ways: it is thought that external objects are mentally rotated in an allocentric reference frame (object-based transformation), while human hands and scenes activate an egocentric reference frame (perspective taking) (Kessler and Thomson, 2010; Kozhevnikov et al., 2006; Zacks and Michelon, 2005).

Several studies with young adults showed that for all three categories reaction times increase with the angular deviation of the object from the normal upright position (Dalecki et al., 2012; Ionta et al., 2007; Kessler and Thomson, 2010; Shepard and Metzler, 1971; Thomas et al., 2013). Moreover, it has been shown that the direction of deviation, namely clockwise or counter-clockwise, has no impact on the reaction times. Discriminating between a right and a left hand proceeds the fastest when the hand is presented fingertips-up, and slowest when it is presented fingertips-down. However, no differences in judging the left of the right hand could have been shown (Dalecki et al., 2012; Simone et al., 2013; Thomas et al., 2013). Furthermore, it has been shown that mental rotation of internal objects is performed faster and more accurate than of external objects (Amorim and Stucchi, 1997; Dalecki et al., 2012; Keehner et al., 2006; Thomas et al., 2013; Wraga et al., 1999).

Behavioral studies investigating mental rotation in older adults found similar results (Gaylord and Marsh, 1975; Saimpont et al., 2009; Simone et al., 2013) and the increase of reaction times with angular deviation was even more pronounced in older participants (Band and Kok, 2000; Dror and Kosslyn, 1994; Gaylord and Marsh, 1975; Saimpont et al., 2009; Simone et al., 2013). Furthermore, even in the normal upright condition older participants had longer reaction times and produced more errors (Band and Kok, 2000; Dror and Kosslyn, 1994; Gaylord and Marsh, 1975; Saimpont et al., 2009). This possibly reflects age deficits for both, the cognitive ability of mentally rotating objects and the ability of judging the objects.

Cognitive deficits in older adults are associated with structural decline, which is most pronounced in frontal areas but also is substantial in parietal areas and the corpus callosum (Dennis and Cabeza, 2011). This degeneration entails a reduced efficiency of structural networks and in consequence functional networks are affected by aging as well. More precisely, lower as well as higher functional coupling has been observed with aging and the associated cognitive decline (Antonenko and

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Abbreviations: NR, no rotation; IR, intermediate rotation; FR, full rotation; *k*, costs; E_{global}, global efficiency; E_{local}, local efficiency; Frontal_{left}, left frontal intrahemispheric network; Frontal_{right}, right frontal intrahemispheric network; Frontal_{inter}, frontal interhemispheric network; Parietal_{left}, left parietal intrahemispheric network; Parietal_{right}, right parietal intrahemispheric network; Parietal_{inter}, parietal interhemispheric network.

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Flöel, 2014; Andrews-Hanna et al., 2007; Geerligs et al., 2014; Wen et al., 2011).

One possibility to investigate functional network organization is the graph theoretical approach (Bullmore and Sporns, 2009), where a network is defined by nodes (vertices, e.g. EEG electrodes) and edges (connections between different vertices) (Bullmore and Sporns, 2009; Rubinov and Sporns, 2010). The topography of such brain functional networks is neither completely regular nor completely random — they are so-called "small-world networks" (Achard and Bullmore, 2007; Latora and Marchiori, 2001). Small-world networks are characterized by dense or clustered local connections and only a few long-range connections (Bassett and Bullmore, 2006; Watts and Strogatz, 1998). Such architecture minimizes the path length between nodes, and thus reduces the costs of processing. Achard and Bullmore (2007) investigated the network efficiency and costs in older participants during resting state using fMRI. Efficiency has been defined as a function of the minimum path length between regions. Costs have been defined as the number of connections within the network. In fact, they found a reduced efficiency in frontal as well as temporal and subcortical regions in older adults compared to young adults. Also, Wen et al. (2011) found a decreased efficiency of the corticocortical network in older adults. This decrease of network efficiency may be a sign of neural dedifferentiation, characterizing a less specialized but more diffused pattern of functional connections (Antonenko and Flöel, 2014; Baltes and Lindenberger, 1997; Park and Reuter-Lorenz, 2009).

The purpose of the present study was to investigate functional network connectivity of frontal and parietal areas in the elderly compared to young participants during a mental rotation task considering the results of Thomas et al. (2013). Additionally, the focus is on discriminating between different object categories. In this study, we investigated the functional connectivity within and between frontal and parietal areas during mental rotation focusing on young adults using EEG measurement. In contrast to the previously mentioned study, now a graph theoretical approach was used in order to analyze the small-world brain network behavior of older compared to younger adults during a mental rotation task.

2. Methods

Ten younger (25.7 ± 1.3 years, 5 male) and ten older volunteers (73 ± 2.5 years, 6 male) participated in this study. The older participants were recruited via a registration list of interest in participating in aging studies. All were free of sensorimotor dysfunctions except for corrected vision, and none of them reported prior experience in mental rotation research. All participants signed an informed consent statement 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. The set-up of the experiment was similar to the former study (Thomas et al., 2013). For detailed description please consider this publication.

2.1. Mental rotation

As in the former study participants attended in three different mental rotation conditions: condition letter ("G" and "R"), condition hand (left or right hand) and condition scene (images of a person sitting at a round table a weapon lying in front) (Fig. 1A). Participants' task was to judge whether the letter was non-reversed or mirror-reversed, they saw a left or right hand and whether the weapon in the scene was on the left or right hand side of the person. To discriminate between the object presentation participants were instructed to press a key either with the right ('k' on the keyboard) or left index finger ('d' on the keyboard). 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. In each condition 144 different stimuli were presented. Each stimulus was displayed until participants responded, and was followed by a randomly varying inter-trial interval of 0.5 s to 1 s.

For statistical analysis the reaction time (RT) between stimulus onset and key press was averaged across clockwise and counterclockwise orientation angles, because no differences have been detected between these orientations, what was in line with the results of previous work (Dalecki et al., 2012; Thomas et al., 2013). Additionally, RT was averaged across the two respective stimulus shapes of each condition ("G" and "R", two different hands, gun or knife), and across repetitions. RT data was submitted to an analysis of variance (ANOVA) with the within-factors Condition (LETTER, HAND, SCENE) and Rotation (0°, 30°, 60°, 90°, 120°, 150°, 180°). The outcome was Greenhouse–Geisser adjusted if necessary, and significant effects were scrutinized by Fishers LSD post-hoc tests. Additionally, the error rate (ER) was calculated as the percentage of wrong answers in the entire presented stimuli separately for each group averaged across all conditions and rotations. ER was submitted to an independent t-test.

2.2. EEG

EEG signals were recorded by 64 electrodes (10–20 systems) (Jasper, 1958) (see also Thomas et al., 2013). In contrast to the former study 1000 ms segments instead of 800 ms segments relative to the stimulus onset (0 to 1000 ms) of the mental rotation task were used. All segments were subdivided according to the 7 different rotation angles from 0° to 180 °. The signals were transformed in the frequency domain 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). 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 participant in the gamma frequency band (30–45 Hz). Different networks have been defined to differentiate between intrahemispheric and interhemispheric as well as between frontal and parietal connections. The different networks considered the coherence values of the following electrode pairs, which were Fisher-Z transformed:

1. For intra-hemispheric networks:

    a. Frontal, left ($\text{frontal}_{\text{left}}$): all possible connections within section I of Fig. 1
    b. Frontal, right ($\text{frontal}_{\text{right}}$): all possible connection within section II of Fig. 1
    c. Parietal, left ($\text{parietal}_{\text{left}}$): all possible connections within section III of Fig. 1
    d. Parietal, right ($\text{parietal}_{\text{right}}$): all possible connections within section IV of Fig. 1

2. For inter-hemispheric networks:

    a. Frontal ($\text{frontal}_{\text{inter}}$): all possible connections between Sections 1 and 2
    b. Parietal ($\text{parietal}_{\text{inter}}$): all possible connections between Sections 3 and 4

As a next step unweighted binary matrices for each participant and each rotation angle separated for each defined network were prepared with a threshold of 0.4. Thus, in total 42 matrices per participant were produced (7 rotation angles × 6 networks). To quantify the network quality structure we used graph theoretical analyses, where a network