Developmental aspects of parietal hemispheric asymmetry during mental rotation

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Introduction

The cognitive process of imagining the representation of an object turning around is called mental rotation [1] and constitutes an important aspect of the general class of spatial transformations as well as a critical ingredient in spatial intelligence. Mental rotation seems to be a cognitive process implemented in the parietal cortex (e.g. [2]), that is working in a continuous, analog way [3].

Many authors have suggested that the process of mental rotation should be understood as fundamentally lateralized to the right hemisphere [4]. The empirical evidence [5], however, suggests that this idea has to be at least qualified: the hemispheric asymmetry seems to be critically dependent upon a number of factors like the participant’s (i) sex [6], (ii) handedness [7], (iii) spatial intelligence [8], and (iv) sex steroid level [9], as well as (v) the dimensionality of the rotation [10], and (vi) the difficulty of the task [11]. Moreover, the pattern of data seems almost wilfully unsystematic, because these factors seem to interact in complex ways. One hypothesis that is able to integrate some of these effects emphasizes the distinction between a holistic process capable of mentally rotating the stimulus representation as a whole that might preferentially engage the right hemisphere, and an analytic process of mentally rotating the stimulus in a piecemeal fashion that is more likely to involve the left hemisphere [5,12]. Which of the two strategies is used (to what degree) might depend on both subject variables like spatial intelligence and task variables like the complexity of the stimuli in the following way: if task complexity is sufficiently low and if participant’s competence is sufficiently high, then the representation is thought to be mentally rotated in a holistic way preferentially activating the right hemisphere. If, however, the task is complex and/or the participant’s competence is low, then the representation is thought to be mentally rotated in a piecemeal fashion preferentially activating the left hemisphere.

Unfortunately, little is known about the development of hemispheric laterality. The field of developmental cognitive neuroscience would substantially profit from exploring the question of hemispheric specialization, especially given the accumulated knowledge we now have regarding, on the one hand, the information processing basis of the cognitive act and, on the other hand, its neural implementation.

The investigation of the development of hemispheric specialization, however, critically depends on a method for measuring hemispheric asymmetry during mental rotation that (i) is specific to the process of mental rotation, (ii) allows utilization of the fine-grained task analysis established by Experimental Psychology, (iii) is simple and cheap enough to realize sufficient sample sizes and (iv) is suitable to be applied to children as young as 6 or 7 years of age, or even younger. Fortunately, event-related potentials (ERPs) indeed fulfill these requirements, and it is, therefore, surprising that they had not yet been recorded during mental rotation under a developmental perspective.

In studies with adults, it was found that in a mental rotation task, the ERP amplitude is systematically related to the orientation of the stimulus: the stimulus-evoked positivity becomes relatively more negative (or less positive) with increasing angular disparities from the upright [13]. Therefore, it was suggested [13] that the decrease of the
positivity is caused by an increase of a slow negativity that should be understood as an electrophysiological correlate of the mental rotation process itself. This idea was validated in a large number of studies with adults, suggesting that the ERP effect observed during mental rotation is indeed highly specific to the mental rotation process itself [14,15].

Therefore, it was the first goal of our study to investigate the ERP effect during mental rotation of letters from a developmental perspective. Additionally, we aimed to investigate the development of hemispheric activation of the mental rotation process in detail. We used letters as stimuli because ERP effects for adults with these stimuli are well established [14]. Additionally, these stimuli do have advantages from an ERP point of view: the variance of response times (RTs) (and of the duration of cognitive processes) will be relatively small and as a consequence, the potential will be relatively concise. Moreover, because only a single stimulus has to be presented, eye movements as a potential source of artifacts will be minimized.

Methods
Participants
Twenty-four children (mean age: 7.6 years), 24 juveniles (11.4 years) and 24 adults (23.8 years) participated in this study. The gender ratio was balanced in each age group. Before testing, all parents gave their informed written consent for children’s participation. The local ethics committee approved the experimental procedure.

Materials and procedure
In each trial, one of the letters F, P, R, and L was presented in their normal or mirror-image version at either 30, 90 or 150° clockwise or counterclockwise from the vertical upright on a computer screen. The letters had a height of 3.2 cm, subtending 2.28° of visual angle. Each trial began with the presentation of a fixation point in the center of the computer monitor. One second later, a letter was presented in the center of the screen for 1.5 s for the adults and for 2.5 s for children and juveniles. To indicate whether the response was correct (incorrect) a + (–) was displayed for 500 ms. Participants were instructed to respond as fast as possible, but accuracy was stressed in the instruction. Trials were separated by randomly varying intervals of 1–3 s.

Letters were presented in blocks of 48 trials each. Each combination of orientation, version and letter occurred eight times resulting in 384 experimental trials. To familiarize participants with the task, 48 unrecorded practice trials were added. Participants pressed the left or right mouse button depending on whether the letter was normal or mirror-reversed. Participants were instructed to avoid eye and other body movements during the recording of the electroencephalogram.

Electroencephalogram analysis
The electroencephalogram was recorded monopolar, with Ag/AgCl electrodes from frontal (Fz), central (Cz) and parietal (left: P3; midline: Pz; right: P4) leads with digitally averaged earlobes as reference. Horizontal and vertical eye movements were monitored by two channels. The left mastoid served as ground. Electrode impedance was kept below 5 kΩ. Band pass was set from DC to 40 Hz; the digitization rate was 250 Hz. All trials were inspected off-line, and those contaminated with artifacts (blinks, eye or other body movements) – less than 30% on average – were rejected. From the edited set of raw data, we extracted ERPs by averaging single trials with correct responses separately for participants, electrodes and experimental conditions.

Statistical analysis
Error rates and RTs were tested statistically in an analysis of variance (ANOVA) including the between-subject factors ‘age group’ and ‘sex’ as well as the within-subject factor ‘orientation’ (30, 90, 150°). For the ERPs, the average amplitude of the epoch 300–700 ms after letter presentation [15] was used as dependent variable, referenced to a prestimulus baseline of 250 ms duration. Statistical effects were tested in an ANOVA including the between-subject factors ‘age group’ and ‘sex’ as well as the within-subject factors ‘orientation’ and ‘electrode position’ (Fz, Cz, P3, Pz, P4). We corrected the significance levels of all ANOVA results to compensate for nonsphericity of the data.

Results
For error rates, main effects of age group [F(2,66) = 28.18] and orientation [F(2,132) = 53.94], as well as an interaction of these two factors [F(4,132) = 5.80; all P < 0.01], were observed. Error rates decreased with age and increased with angular displacement from the upright. The latter effect was present in all three age groups, was also larger if the participant is younger [F(4,132) = 5.36; P < 0.01]. Moreover, the amplitude of the positivity decreased with increasing angular displacement from the upright [F(4,132) = 76.44] and of orientation [F(2,132) = 295.32; both P < 0.01] were observed, but no interaction of these two effects [F(4,132) = 1.80; P > 0.15]. RT decreased with age (1282 vs. 1057 vs. 799 ms) and increased with angular displacement from the upright (944 vs. 1043 vs. 1158 ms).

Event-related potentials
Main effects of age group and orientation, as well as the interaction of these two factors, turned out to be reliable at all electrodes, with the most pronounced effects at parietal leads. Presentation of the letter evoked a large positivity (see Fig. 1). The amplitude of the ERP was larger for younger participants [F(2,66) = 42.72; P < 0.01]. Moreover, the amplitude of the positivity decreased with increasing angular displacement from the upright [F(2,132) = 107.58; P < 0.01]. This effect, present in all three age groups, was also larger if the participant is younger [F(4,132) = 5.56; P < 0.01]. To test for the laterality of the effect, an additional ANOVA was run with factors ‘age group’ and ‘sex’ as between-subject effects, and ‘orientation’ and ‘laterality’ (electrode positions P3 vs. P4) as within-subject effects. In addition to the main effects and two-way interactions, a three-way interaction was found [F(4,132) = 2.96; P < 0.05]. The amplitude modulation as a function of letter orientation was found to be substantially lateralized to the left hemisphere for the children [F(2,44) = 6.38; P < 0.01], only numerically so, for the juveniles [F(2,44) = 1.73; P > 0.15], but was found to be completely bilaterally present for the adults [F(2,44) = 0.55] (see Fig. 2).
Discussion

The results of this first study regarding the developmental aspects of ERP effects during mental rotation are straightforward: the amplitude modulation as a function of mental rotation was not only replicated with adults, but was also observed for the first time with children as young as 7 or 8 years. Much more data are needed with comparable stimuli and procedures to find an explanation for the larger overall amplitudes, as well as the larger amplitude effect for the children. Under some conditions, ERP amplitudes increase, decrease or are not affected by age [16]. Nevertheless, the finding of an amplitude modulation of the ERPs as a function of letter orientation even with children is indeed fascinating. The ERP effect was previously shown to be functionally related directly to the process of mental rotation [14]. Future studies will allow investigation of the development of the neural correlate of mental rotation in detail utilizing the fine-grained task analysis established in Experimental Psychology.

The most important effect, however, is that in children left amplitude modulation was substantially greater than that of the right hemisphere and this difference was absent in adults. This result suggests that the development of mental rotation should be understood as a function that becomes more and more independent of processes localized in the left hemisphere. One might be tempted to trace back this finding to the difficulty of the task being greater for younger participants. To test this idea, we calculated the correlations between the laterality of the ERP effect and (i) participant's overall error rate and (ii) the increase of the error rate with increasing angular displacement. These correlations were run separately for each age group as well as for the whole sample. Out of these eight correlations indicating the effect of the difficulty of the task being greater for younger participants, not a single one turned out to be reliable ($-0.17 < r < 0.29$; all $P > 0.15$). Therefore, the ‘simple explanation’ that the left hemisphere effect is greater than that of the right hemisphere in children as a consequence of the greater difficulty of the task for the children is not supported by the data.

An alternative explanation [5,12] suggests that the left hemisphere is involved in more complex, piecemeal strategies of mental rotation, whereas the right hemisphere...
is preferentially engaged when the representation, as a whole, is mentally rotated. This would suggest that cognitive development leads to a more holistic rotation process. More studies are needed to evaluate the development of hemispheric asymmetry during mental rotation in detail, as well as the idea that cognitive development leads to a more holistic mental rotation process.

**Conclusion**
The present data suggest that the cognitive development during mental rotation might be characterized as a function that becomes more and more independent of processes localized in the left hemisphere.

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**References**