Effects of dynamic rotation on event-related brain potentials

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Abstract

Event-related potentials were recorded during a mental rotation task. Subjects were shown pairs of letter-like shapes and were asked to make a parity judgment. The shape on the left was always in its canonical position and the shape on the right could either be in its canonical position or be a mirror image. Two variables were manipulated for the shape on the right. First, it could appear at different orientations (50°, 100° or 150°); second, it could be presented in a stationary position, in a dynamic congruent direction (the shape slowly rotating toward its normal upright position) or in a dynamic incongruent direction (the shape slowly rotating in the opposite direction to its normal upright position). Orientation- and direction-dependent modulations of a negative slow wave were found. For orientation, the typical amplitude effect over parietal sites was found, the amplitude becoming more negative as the rotational angle increased. For direction, the amplitude of the negative slow wave was larger for stationary and dynamic incongruent trials than for dynamic congruent trials at 100° and 150°. This result suggests that presentation of a stimulus in a dynamic congruent direction facilitates the mental rotation process. At 50°, differences between dynamic incongruent trials and both stationary and dynamic congruent trials were found, suggesting that the incongruent movement elicits an obstructing effect over the mental rotation process. In summary, the present experiment provides new evidence in support of the idea that the amplitude modulation over the parietal cortex is a psychophysiological marker of the mental rotation process.

1. Introduction

Mental rotation is a process that has been extensively investigated by cognitive psychologists. It was first described by Shepard and Metzler\textsuperscript{[20]} in an experiment where pairs of drawings of three-dimensional nonsense shapes were presented, and subjects were asked to make a parity judgment: that is, they were required to decide whether drawings were the same or if one was a mirror image of the other. Shepard and Metzler found that the time taken to decide on the parity of a shape increased monotonically with the angular disparity of their orientation in space. Since then, the same results have been repeatedly reported; the mental rotation effect has been demonstrated with alphanumeric characters, polygons, letter-like symbols, and common objects\textsuperscript{[2,5,12]}. This increase in reaction time depending on angular disparity has been taken as evidence that the system rotates mental representations in order to put them in their normal position. Moreover, the subjects themselves have reported from their own introspections that they used mental rotation to perform tasks of this kind. Therefore, mental rotation has been considered a cognitive process that is isomorphic to physical rotation: it is
suggested that subjects rotate images in their minds as they would rotate physical figures in the real world.

Studies with event-related potentials (ERPs) have reported the existence of a psychophysiological marker of the mental rotation phenomenon. This marker is a slow parietal negativity with latency between 400 and 800 ms, whose amplitude is modulated by the amount of mental rotation performed by the subject. The amplitude of this negative wave becomes larger as the angular disparity from the right increases. The rotation-related negativity was first described by Peronnet and Farah [16], Wijers et al. [21], and Rössler et al. [18], who equated late negativity with the cognitive process of mental rotation. Although these authors used alphanumeric characters as stimuli, the same negativity modulation has been reported in other experiments using different shapes [11,15,19,22].

A psychophysiological correlate of a cognitive process would be particularly useful for broadening our knowledge of human cognition. This ERP effect is a candidate, and several experiments have been performed to establish its functional significance (for a review, see Ref. [6]). If a functional significance is established between mental rotation and the slow parietal negativity, the amplitude modulation of this component could be used as an indicator of the presence of mental rotation itself. The substantial body of research conducted by Heil et al. has provided compelling evidence of the functional significance of the rotation-related negativity. This evidence can be summarized in two sets. One series of experiments manipulated the presence or absence of the mental rotation process in order to perform a task [8,10]. Alphanumeric characters were presented in different orientations, and the type of task was manipulated so that its performance did or did not involve mental rotation. Obviously, if the amplitude modulation of the slow negativity was a psychophysiological marker of mental rotation, it would be absent if mental rotation was not used to solve the task. The results confirmed this prediction.

On the other hand, the functional significance of the slow negativity wave would also be supported if delaying the mental rotation process also delayed the onset of the amplitude modulation. Heil and Rolke’s experiment [7] confirmed this point. The mental rotation process was delayed by manipulating the duration of perceptual encoding of the stimuli and by manipulating character identification and discrimination. In compliance with the sequential model of information processing, both processes were performed before the mental rotation process began. Heil and Rolke [7] provided empirical evidence for the temporal relationship between the cognitive process of mental rotation and the onset of the amplitude modulation of the slow negative wave.

The goal of the present study was to add new evidence to support the idea that the amplitude modulation of the ERPs over the parietal cortex is a psychophysiological correlate of the mental rotation process. As it has been proposed that mental representations of objects are rotated through a trajectory in much the same manner that physical objects are rotated, it may be that the manipulation of perceived rotation will affect the mental rotation process. Jolicoeur and Cavanagh [13] investigated the relationship between perceived rotational motion and mental rotation by measuring reaction time. In a parity judgment task, they presented characters that moved either in the direction of mental rotation (congruent trials) or in the opposite direction (incongruent trials). An effect of congruency was reported on reaction time. Whereas incongruent trials resulted in slower response times, congruent trials showed a faster response. It seemed that a character rotation in the opposite direction interfered with the subject’s ability to perform mental rotation, while no interference but facilitation was found in trials in which the direction of character rotation was the same as the postulated direction of mental rotation. It is suggested that the congruency effect takes place throughout mental rotation rather than simply delaying its onset. These results have been replicated by Heil et al. [9] using characters as stimuli, by Jolicoeur et al. [14] using drawings of common objects, and by Corballis and Blackman [3] and Corballis and Corballis [4] using small bars.

In the present experiment, subjects were engaged in a parity task in which a pair of letter-like shapes was presented simultaneously: the shape on the left of the screen appeared in its normal version and the shape on the right could be presented either in its normal version or as a mirror reflection. Subjects had to compare the shapes and decide if they were identical in shape or if they were mirror images of each other. The shape on the right was shown in different orientations (50°, 100°, and 150° from its normal upright position) and in different directions (stationary, dynamic congruent—the shape rotated slowly towards the normal upright—or dynamic incongruent—the shape rotated slowly in the opposite direction to the normal upright). By manipulating the direction, we expected to influence the mental rotation process. On the one hand, it is reasonable to assume that when a stimulus slowly rotates toward its canonical position, the mental rotation process will be facilitated—given that the process of mental rotation is assumed to be isomorphic to the physical rotation, and so the rotation-related negativity will turn out to be less negative. On the other hand, when a stimulus slowly rotates against its canonical position, the same argument may apply. In this case, the mental rotation process will be impeded because the shape rotates in the opposite direction to the one that shortens the distance to the upright, and therefore, the amplitude of the rotation-related negativity will become more negative. In summary, if the amplitude of the slow negative potential is an index of the mental rotation process,
we expect to find an effect of direction on the ERP amplitude: the amplitude will be more negative for the dynamic incongruent stimuli, medium for the stationary stimuli, and less negative for the dynamic congruent stimuli.

2. Materials and methods

2.1. Participants

Ten healthy, right-handed volunteers (seven women) took part in the experiment. Age ranged from 18 to 26 years, (mean ± SD 19.9 ± 2.3). Handedness of the subjects was evaluated by self-report. All participants were university students and had normal or corrected-to-normal visual acuity. Written informed consent was obtained from all participants prior to the start of the experiment.

2.2. Stimulus materials

Pairs of three-dimensional letter-like shapes were used as stimuli (see Fig. 1), and were presented using a Pentium IV computer and a 17 in. SVGA monitor. Each pair consisted of a shape presented in its normal version on the left of the computer screen and another shape presented in its normal or mirror-image version on the right of the screen. The shapes were presented simultaneously. In the shape on the right, two variables were manipulated: first, this shape could appear at 50\(^\circ\), 100\(^\circ\) or 150\(^\circ\) clockwise from the vertical upright and second, it could be presented in a stationary position, in a dynamic congruent direction (the shape was moved smoothly rotating clockwise) or in a dynamic incongruent direction (the shape was moved smoothly rotating counter-clockwise). Both dynamic congruent and dynamic incongruent shapes were presented at a 25\(^{\circ}\)/s angular velocity on the screen. Although a zero degrees condition is usually used in mental rotation experiments, this condition was not included in the present experiment because it is not possible to combine it with the movement conditions (dynamic congruent and dynamic incongruent direction). The inclusion of a zero degrees condition would increase the number of trials in the stationary conditions by 25% as compared to the dynamic conditions. Hence, dynamic conditions would occur at a comparatively low frequency and, therefore, might give rise to a P3b component (for a review see [17]). Because the P3b component has similar latency as the rotation-related negativity, the movement effect upon the ERP might be obscured.

Stimuli were shown in green on a white background (luminance 110 cd/m\(^2\)), and subtended a vertical visual angle of 1.72\(^\circ\) and a horizontal visual angle of 1.33\(^\circ\). The programme language used to run the experiment was C++/Open GL, a software interface for 3D graphics with hardware developed by Silicon Graphics, Inc.

2.3. Procedure

Participants were seated in an electrically-shielded, sound-attenuating room at a distance of 150 cm from the display screen, whose center was at eye level. The session began with a training period consisting of the presentation of trials similar to those used in the recording period. To be sure that subjects clearly understood the task to be performed, the training period finished when the participant had correctly answered eight consecutive trials. Participants achieved this criterion in a few trials.

When the training period was over, the recording period started. Subjects were instructed to relax and to keep their eyes on the screen. They were also told that it was important to avoid blinking, and that if they needed to blink, they should try to wait until a question mark or a rest message appeared on the screen. Each trial began with the presentation of a red fixation point in the center of the screen for 500 ms. A stimulus was then presented for 2 s. After that, a question symbol was displayed in the center of the monitor. The inter-trial interval was 1000 ms. Subjects were required to determine whether the shape on the right was a normal or a mirror-reversed version of the shape on the left. They had to indicate their decisions after the question symbol by pressing the corresponding mouse keys, with responding fingers being counterbalanced across subjects.

Twelve blocks of 72 trials were presented to each participant. A message indicating a 1-min rest appeared on the screen after each block, and there was a 15-min rest in the middle of the recording session. The type of trials was controlled within each block in such a way that a block included trials resulting from the combination of direction (stationary, dynamic congruent, and dynamic incongruent), orientation (50\(^\circ\), 100\(^\circ\), and 150\(^\circ\)), version (normal and mirror-reversed), and type of stimulus (four letter-like shapes). Each type of trial was randomly presented in every block. All participants were tested on 864 trials, 48 for each experimental condition.

2.4. Electrophysiological recording

EEG was recorded with the SynAmps/SCAN 3.0 hardware and software (NeuroScan, Hemdon, VA) from 31 tin electrodes mounted in a commercial electro-cap (Electro-Cap International, Eaton, OH). Nineteen electrodes were positioned according to the 10–20 International...
System: three electrodes were placed over midline sites at Fz, Cz, and Pz locations, along with 8 lateral pairs of electrodes over standard sites on frontal (FP1/FP2, F7/F8, F3/F4), central (C3/C4), temporal (T3/T4, T5/T6), parietal (P3/P4), and occipital (O1/O2) positions. Two electrodes were placed at Fpz and Oz, and ten electrodes were placed halfway between the following additional locations: fronto-central (FC1/FC2), fronto-temporal (FT3/FT4), centro-parietal (CP1/CP2), temporo-parietal (TP3/TP4), and mastoids (M1/M2). The common reference electrode for EEG measurements was placed on the tip of the nose. EEG channels were continuously digitized at a rate of 500 Hz by a SynAmp™ amplifier (5083 model, NeuroScan, Herndon, VA). A band pass filter was set from 0.05 to 30 Hz, and electrode impedance was always kept below 5 kΩ. For monitoring eye movement and blinks, FP1, FP2, FPz, and an electrode placed at the external canthi of the right eye were used.

2.5. Data analysis

Error rate was analyzed by means of repeated measurements ANOVA taking as factors direction (stationary, dynamic congruent and dynamic incongruent), orientation (50°, 100°, and 150°) and version (normal and mirror-reversed). Reaction times were not recorded in the present experiment because subjects were to respond only after the question mark appeared on the screen in order to avoid a contamination of the ERP by response related activity.

As for the electrophysiological data, epochs for each subject in each experimental condition were averaged relative to a pre-stimulus baseline that was made up of the 100 ms of activity preceding the epoch of interest. Trials with artifacts (voltage exceeding ±75 μV in any channel) and trials with incorrect behavioral responses were excluded from the ERP average. The mean number of epochs included in each ERP average varied between 72.8 and 79.9 for the various types of stimuli used (as the version factor did not produce any significant difference, the data were averaged ignoring this factor), and the minimum number of epochs included in any individual average was 57. ERP data were analyzed by computing the mean amplitude in 50 ms windows from 500 to 1000 ms post-stimuli. The purpose of working with this large range of latency windows was to identify the time interval where the electrophysiological differences between experimental conditions began, where these differences finished, and where they reached their maximum amplitude.

A 3 × 3 × 2 × 3 × 5 repeated-measures analysis of variance (ANOVA) was performed on the ERP amplitude at 15 electrodes (F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6) taking as factors direction (stationary, dynamic congruent, and dynamic incongruent), orientation (50°, 100°, and 150°), version (normal and mirror-reversed), frontality (frontal, central, and parietal) and laterality (five levels from left to right). Repeated-measures ANOVAs were carried out with the Greenhouse–Geisser correction for sphericity departures, which was applied when appropriate. The F value, the probability level following correction, and the ε value are reported. Whenever a main effect reached significance, t tests contrasts were calculated and the Hochberg approach was used to control for the increase in type I error. Simple effects were calculated in order to analyze significant interactions. Finally, trend analyses were performed to try to fit a linear trend between amplitude and orientation.

3. Results

3.1. Behavioral data

Error rate analysis showed that there were not differences in accuracy between conditions; no main effect or interaction reached significance (all P values > 0.05). The absence of differences might be due to the fact that subjects were not asked to answer as quickly as possible, but after a question symbol appeared on the screen. As a consequence, subjects might have had enough time to think about their answer and therefore, subjects had a few errors. Table 1 shows means of error rate and standard deviations for the three orientations in stationary, dynamic congruent, and dynamic incongruent stimuli.

3.2. Electrophysiological data

Fig. 2 shows the grand average ERPs for the different orientations in the stationary position, the dynamic congruent direction, and the dynamic incongruent direction at P3, Pz, and P4. The usual pattern of voltage for the orientation effect in the stationary position and in the dynamic congruent direction can be seen: the greater the degree to be rotated, the more negative the amplitude of the slow wave. However, this pattern changed in the dynamic incongruent direction, where these amplitude differences were not present. In Fig. 3, the same ERPs as Fig. 2 are rearranged so as to show the slow wave modulation as a function of the stimulus direction—grand average ERPs are shown at the different directions for 50°, 100° and 150°. A direction-dependent modulation of the amplitude of the slow wave can be distinguished in Fig. 3. As for 50° and 100°, the voltage of this slow wave was more positive for the dynamic congruent direction, medium for the stationary

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Means of error rate and standard deviations (in brackets) for the three orientations in stationary, dynamic congruent, and dynamic incongruent stimuli</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50°</td>
</tr>
<tr>
<td>Stationary</td>
<td>0.01 (0.02)</td>
</tr>
<tr>
<td>Dynamic congruent</td>
<td>0.02 (0.02)</td>
</tr>
<tr>
<td>Dynamic incongruent</td>
<td>0.03 (0.04)</td>
</tr>
</tbody>
</table>
Fig. 2. Grand average ERPs ($n = 10$) for the different orientations in the stationary position and in both dynamic directions at P3, Pz, and P4.

Fig. 3. Grand average ERPs ($n = 10$) for the different directions in 50°, 100° and 150° at P3, Pz, and P4.
position, and more negative for the dynamic incongruent direction. For the 150° orientation, the pattern of voltage was similar to that observed in the other orientations, except for the dynamic incongruent direction; when the stimulus was presented in a dynamic incongruent direction, the amplitude of the negative slow wave was between those of the stationary position and the dynamic congruent direction.

The ANOVA results for the 50 ms windows from 500 to 1000 ms post-stimulus are shown in Table 2. The main effect of direction reached statistical significance in the 500–950 ms interval (P values less than 0.05). t tests contrasts showed that there were amplitude differences between the stationary position and the dynamic congruent direction in the 500–750 ms windows (P values less than 0.007), and differences between the two dynamic directions in the 500–950 ms windows (P values less than 0.017). As for t tests contrasts between the stationary position and the dynamic incongruent direction, all failed to reach statistical significance, although the amplitude average for dynamic incongruent stimuli was more negative than the amplitude average for stationary stimuli.

For a more detailed analysis of the direction effect, complementary analyses were performed in every orientation at P3, Pz, and P4 (Table 3 shows a summary of these results). In the 50° orientation, the following results were found: there were statistically significant differences between the incongruent and congruent directions in the 500–800 ms interval at P3, in the 550–800 ms interval at Pz, and in the 600–700 ms interval at P4; moreover, there were also differences between the stationary position and the dynamic incongruent position in the 500–700 ms interval at P3 and in the 500–600 ms interval at Pz. As for the 100° orientation, differences between the incongruent and congruent directions were found in the 650–950 ms interval at P3, in the 600–1000 ms interval at Pz and in the 600–1000 ms interval at P4; differences were also found between the stationary position and the dynamic congruent direction in the 650–800 ms interval at P3, and in the 600–850 ms interval at Pz and in the 600–800 ms interval P4. Finally, regarding the 150° orientation, only differences between the stationary position and the dynamic congruent direction were found at P3, Pz and P4 in the 850–1000 ms window.

In summary, statistical analysis showed that the direction effect differed depending on the orientation of the stimuli. When the rotational angle was short (50°), amplitude was more negative for the shapes presented in a dynamic incongruent direction than for the shapes presented in a stationary position or in a dynamic congruent direction. It seemed as if at 50°, the movement of the shape towards its normal upright did not facilitate the mental rotation process, whereas the opposite movement impeded it. When the rotational angle was 100°, the ERP pattern was different: amplitude was more positive for dynamic congruent stimuli than for both stationary and dynamic incongruent stimuli. This result suggests a facilitating effect of the congruent movement on the mental rotation process at 100° orientation. Finally, when the orientation was 150°, amplitude was more negative for stationary stimuli than for dynamic congruent stimuli, suggesting again the presence of a facilitating effect over the mental rotation process. However, it must be highlighted that this effect occurred later than the facilitating effect described for 100° orientation.

As for the effect of the orientation on the ERPs, the ANOVA showed that the orientation × frontality interaction reached statistical significance in the 500–950 ms windows, and the direction × orientation × frontality interaction reached statistical significance in the 500–550 and the 650–950 ms windows (see Table 2). Simple effects analysis showed that the orientation effect was only present at central locations in the 600–800 ms post-stimulus, and at parietal locations in the 550–900 ms interval (see results in Table 4).

A detailed analysis of the orientation effect was performed at P3, Pz, and P4, locations where the orientation effect is usually found. This analysis consisted of a trend analysis for the orientation in the stationary position, the dynamic congruent direction, and the dynamic incongruent direction. The following results were found. A linear trend could be adjusted between amplitude and orientation in the

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### Table 2

ANOV A results for the effects that reached statistical significance

<table>
<thead>
<tr>
<th>Time (ms)</th>
<th>Direction</th>
<th>Orientation × Frontality</th>
<th>Direction × Orientation × Frontality</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>e</td>
</tr>
<tr>
<td>500–550</td>
<td>12.185</td>
<td>0.001***</td>
<td>0.896</td>
</tr>
<tr>
<td>550–600</td>
<td>7.099</td>
<td>0.005**</td>
<td>0.822</td>
</tr>
<tr>
<td>600–650</td>
<td>9.912</td>
<td>0.001***</td>
<td>0.923</td>
</tr>
<tr>
<td>650–700</td>
<td>16.806</td>
<td>0.001***</td>
<td>0.826</td>
</tr>
<tr>
<td>700–750</td>
<td>15.381</td>
<td>0.001***</td>
<td>0.973</td>
</tr>
<tr>
<td>750–800</td>
<td>8.352</td>
<td>0.003***</td>
<td>0.981</td>
</tr>
<tr>
<td>800–850</td>
<td>5.538</td>
<td>0.013*</td>
<td>0.974</td>
</tr>
<tr>
<td>850–900</td>
<td>4.157</td>
<td>0.033*</td>
<td>0.944</td>
</tr>
<tr>
<td>900–950</td>
<td>3.721</td>
<td>0.044*</td>
<td>0.922</td>
</tr>
<tr>
<td>950–1000</td>
<td>1.175</td>
<td>0.331</td>
<td>0.973</td>
</tr>
</tbody>
</table>

* 0.05 ≥ P > 0.01.
** 0.01 ≥ P > 0.001.
*** P ≤ 0.001.
500–950 interval for the stationary stimuli, in the 600–800 interval for the dynamic congruent stimuli, and in the 700–800 ms in the dynamic incongruent stimuli (see Results in Table 5). When the stimuli were presented in a stationary position or in a dynamic congruent direction, the results are the same as those described in the literature: the greater the degree to be rotated, the more negative the amplitude of the slow wave. However, when the direction was dynamic incongruent, the main effect of orientation could only be described by a linear trend in the 700–800 interval. In order to analyze the effect of the orientation in the dynamic incongruent direction, $t$ test contrasts were performed and differences were only found between 50° and 150° (all $P$ values less than or equal to 0.02). As a consequence, it can be concluded that the typical orientation effect was not elicited when the shape was presented in a dynamic incongruent direction.

4. Discussion

The present study examined the effect of mental rotation on event-related potentials. Previous studies with ERPs, where objects and characters were shown in different orientations, have reported the presence of a slow negative potential related to the mental rotation process (for a review, see Ref. [6]). The increased negativity of the amplitude of ERPs over the parietal cortex depending on the rotational angle necessary to place the object in its normal upright position gave support to the idea that this modulation of the amplitude is an index of mental rotation itself. To date, mental rotation using ERPs has been studied exclusively with stationary stimuli. In the present experiment, the study of mental rotation was tested with dynamic stimuli.

Our results confirmed those reported in previous studies with stationary stimuli. When the stimuli were presented in a stationary position the slow negativity increases linearly as a function of the angular disparity of the stimuli from the upright. Moreover, this effect was larger at parietal locations, as usually reported in mental rotation research. However, the most important aspect of the present experiment is the effect of dynamic rotation on the ERPs. Reaction time studies [3,4,9,13,14] have reported both facilitation and obstruction of the mental rotation process associated with motion of the characters and objects. Trials with incongruent motion increased reaction time, whereas trials with congruent motion reduced it. In the present experiment, we studied whether the same phenomenon can be described by means of ERPs. In other words, we aimed to examine whether the amplitude of the rotation-related negativity would be affected by the congruent or incongruent movement of the stimulus. If a movement effect could be demonstrated, this would provide further support for the idea that the amplitude modulation of the parietal negative wave is a psychophysiological marker of mental rotation.

Our results agree at least to some extent with those reported in reaction time studies for the movement effect over the mental rotation process. A direction effect over the ERPs amplitude was found. However, this effect depended on the orientation of the stimuli. When the stimulus was presented at 50° orientation, only the obstructing effect could be described. The amplitude of the slow negative wave was larger for the dynamic incongruent stimuli than for both the stationary and the dynamic congruent stimuli. This negativity increase may have been due to an obstruction of the mental rotation process because the perceived rotation was divergent from mental rotation. Although this result agrees with those reported in reaction time studies (a longer reaction time for incongruent stimuli), the expected facilitation effect over mental rotation for the dynamic congruent stimuli was not found. ERPs results showed no differences between the dynamic congruent and the stationary stimuli, suggesting that there was no facilitation of the mental rotation process when the stimuli moved toward their canonical position. This unexpected result may be due to the fact that when the angle to be mentally rotated is small (50°), the task would be too easy to be facilitated by the congruent movement. In fact, it is often found that for short rotations, there is no difference from the upright condition either behaviorally or in the ERPs (for example, Bajric et al. [1] did not find differences in the ERP amplitude between 0° and 45° in the ERP slow wave in a parity judgment task; Cooper and Shepard [2] reported mental rotation for mirror/normal letter discriminations and also found this lack of linearity for reaction time near the upright). As a consequence, it has been suggested that mental rotation might not be necessary to make a parity judgment at short angular disparities. This might explain the absence of facilitation effect in the present experiment.

Regarding the 100° orientation, the results closely matched the predictions except for the lack of statistical significance in the dynamic incongruent vs. stationary

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### Table 3

<table>
<thead>
<tr>
<th>Contrast</th>
<th>50°</th>
<th>100°</th>
<th>150°</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P3</td>
<td>Pz</td>
<td>P4</td>
</tr>
<tr>
<td>Inc–Cong</td>
<td>500–800</td>
<td>550–800</td>
<td>600–700</td>
</tr>
<tr>
<td>Inc–Sta</td>
<td>500–700</td>
<td>500–600</td>
<td>–</td>
</tr>
</tbody>
</table>

Results are shown for every orientation at P3, Pz and P4.

Inc: dynamic incongruent; Cong: dynamic congruent; Sta: stationary.
Comparison. As predicted, the amplitude of the slow wave was less negative for the dynamic congruent stimuli than for the stationary and the dynamic incongruent stimuli. These results indicate again that the rotating movement modulates the amplitude of the rotation-related negativity, although the ERP pattern is different from that described for the 50° orientation—where only the obstructing effect was found in the statistical analysis. In summary, with 100°, the facilitating effect of the dynamic congruent movement was confirmed, but the obstructing effect of the incongruent movement was not.

Finally, when the angle to be rotated was 150°, again a facilitating effect over the mental rotation process was found, since congruent stimuli were associated with less negativity than stationary ones; however, the predicted opposite effect for the dynamic incongruent stimuli did not occur. As has been mentioned above, there were no differences between dynamic congruent and both stationary and dynamic congruent stimuli.

Concerning these results, one could speculate that the movement effect is not due to the stimulus movement per se, but is a consequence of the orientation effect since, by the time of onset of the mental rotation process, congruent motion will have reduced the angular distance from to upright whereas incongruent motion will have increased it. This possibility can be discarded because of the following reason. It is generally assumed that mental rotation starts at about 400 ms after the stimulus presentation. Dynamic congruent and dynamic incongruent stimuli in the present experiment were presented at a 25°/s angular velocity. Therefore, 400 ms after the stimulus presentation, the stimulus has moved about 10°. An orientation shift of 10° is too small to account for the differences in voltages.

When the orientation effect was analyzed in the stationary position and in both dynamic directions at parietal sites, the typical amplitude modulation was evident when the stimulus was presented in a stationary position—replicating the results previously described in the ERPs literature—and in a dynamic congruent direction. In both cases, the amplitude of the rotation-related negativity became larger as the rotational angle from the upright increased. However, contrary to expectations, the rotation-

<table>
<thead>
<tr>
<th>Time (ms)</th>
<th>Frontal</th>
<th>Central</th>
<th>Parietal</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>ε</td>
</tr>
<tr>
<td>500–550</td>
<td>0.19*</td>
<td>0.035*</td>
<td>0.004*</td>
</tr>
<tr>
<td>550–600</td>
<td>0.02**</td>
<td>0.008*</td>
<td>0.009*</td>
</tr>
<tr>
<td>600–650</td>
<td>0.01**</td>
<td>0.002*</td>
<td>0.003*</td>
</tr>
<tr>
<td>650–700</td>
<td>0.001*</td>
<td>0.0002**</td>
<td>0.0005*</td>
</tr>
<tr>
<td>700–750</td>
<td>0.001*</td>
<td>0.0002**</td>
<td>0.0005*</td>
</tr>
<tr>
<td>750–800</td>
<td>0.01**</td>
<td>0.002*</td>
<td>0.003*</td>
</tr>
<tr>
<td>800–850</td>
<td>0.001*</td>
<td>0.0002**</td>
<td>0.0005*</td>
</tr>
<tr>
<td>850–900</td>
<td>0.001*</td>
<td>0.0002**</td>
<td>0.0005*</td>
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<tr>
<td>900–950</td>
<td>0.001*</td>
<td>0.0002**</td>
<td>0.0005*</td>
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<tr>
<td>950–1000</td>
<td>0.001*</td>
<td>0.0002**</td>
<td>0.0005*</td>
</tr>
</tbody>
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* 0.05 ≥ P > 0.01.
** 0.01 ≥ P > 0.001.
*** P ≤ 0.001.
related negativity modulation was not evident when the stimulus slowly rotated in the opposite direction to its normal upright.

Some explanations for this unexpected result can be drawn as follows. According to Jolicoeur and Cavanagh [13] and Jolicoeur et al. [14], the fact that the reaction time became longer for incongruent stimuli could be caused by a tendency of subjects to mentally rotate incongruent stimuli in the direction of their physical motion and, hence, along the longer of the two possible paths to upright. If subjects acted always in this way, when a stimulus was presented with an incongruent movement, the amplitude of the mental-rotation negativity to 50°, 100°, and 150° would be expected to decrease as the angular departure from the upright increases—because 50° would transform to 310°, 100° would transform to 260°, and 150° would transform to 210°. However, the present experiment showed neither this pattern of amplitude modulation of the mental-rotation negativity nor the pattern expected if the subjects preferred the shorter rotation. Therefore, there is no evidence that subjects chose always the longer way to make the parity judgment.

Although the present experiment allows us to discard the possibility that subjects rotate always the stimulus along the longer way when the stimulus moved against its normal upright, it is plausible to consider the following: subjects might tend to act this way with longer angles—when there is not a large difference between the distance going clockwise or going counterclockwise—and not with shorter angles—when the distance is much longer if subject opted to go clockwise. In the present experiment, differences in the rotation-related negativity were found only between 50° and 150° when a stimulus was presented in an incongruent direction—the amplitude was more negative for 150°. Because no differences were found between 100° and 150°, it might be that participants opted to rotate some stimuli using the longer way and other using the shorter way. If this happened, the expected orientation effect over the ERPs, with these angles, might have been cancelled. Therefore, the orientation effect would not be present in incongruent stimuli. Although this might be a possible explanation, the issue merits further investigation. It is important that in future experiments, subjects are asked to report the direction in which they rotate the items. Another way of investigating this fact is to analyze the time course of the voltage standard deviations rather than the time course of the mean voltages because more variation is expected to be found if subjects use the long way rotations in some trials and the short way rotations in other trials. Unfortunately, raw ERP traces show so much background noise that the increase in variation due to occasional long routes may not be detectable. Overall, ERPs are a useful measure for clarifying the kind of strategy that subjects use to make their decision when there is a discrepancy between perceived and mental rotation.

In conclusion, this study extends previous work on mental rotation and reiterates the effects of angular disparity on ERPs. New support to the existence of a rotation-related negativity as a psychophysiological marker of a cognitive process has been added. The present experiment differs from previous research in that dynamic stimuli were presented in order to facilitate or impede the mental rotation process. The study makes two important contributions. First, it confirms the notion that, with large angular disparities, if a shape is presented slowly rotating to its normal upright, the mental rotation process is facilitated: the typical orientation effect over the amplitude of the ERPs was present, but the amplitude was systematically more positive than those of either stationary or dynamic incongruent stimuli. Second, when a stimulus is presented in a short angular disparity and moved slowly in the opposite direction to its normal upright, the mental rotation process is obstructed. These findings provide empirical evidence that the rotation-related negativity is a psychophysiological correlate of the mental rotation process. In other words, the functional relationship between the process of mental rotation and the rotation-related negativity is validated.

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References