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The time course of planar and non-planar rotations in a letter rotation task

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Highlight

- Mirror-reversed letters rotation involves both planar and non-planar processes
- These processes are engaged at different times for different rotation angles
- The time-course of planar and non-planar rotations differs for each rotation angle

1. Introduction

Mental rotation tasks (MRTs) are widely used to assess people' abilities to rotate the representation of an object in their minds (Shepard & Metzler, 1971). In classic versions of the MRTs, a pair of visual stimuli are presented on the screen with different rotation angles and participants are required to identify whether they are identical or mirror images of one another. Response times (RTs) increase linearly with the increasing rotation angles. This linear increase in RTs, observed in MRTs with various types of stimuli (e.g., 2D polygons, character letters, pictures of hands, etc.), is typically interpreted as evidence that mental representation of the stimuli are rotated in one's minds in a spatial transformation process (mental rotation process; MR) akin to the actual physical rotation of the object (Shepard & Metzler, 1971; Cooper & Shepard, 1973).

Despite the increasing number of studies on MR, the cognitive processes underlying it are not fully understood. One question that is still debated concerns the cognitive processes engaged during the MR of identical and mirror-reversed stimuli. This question has been mostly investigated in MRTs with characters letters. In these tasks, one letter is centrally presented on the screen either in its canonical or mirror-reversed orientation with different rotation angles. Participants have to mentally rotate the letter and to compare it with its canonical representation stored in their long-term memory to determine the letter orientation. In behavioural studies, RTs are longer for mirror-reversed than canonical letters (e.g., Cooper & Shepard, 1973; Kung & Hamm, 2010). To explain the longer RTs observed on mirror-reversed trials, Cooper and

Shepard (1973) suggested that participants prepare for a 'canonical letter' response by default at the beginning of each trial. Therefore, on mirror-reversed trials, this response has to be suppressed before the correct response can be executed. Accordingly, longer RTs for mirror-reversed trials would be caused by longer response selection processes. Others (Provost & Heathcote, 2015; Larsen, 2014) claimed that increased variance in RTs accounted for the longer RTs observed in mirror-reversed than canonical letters.

Alternatively, some researchers have postulated the presence of an additional cognitive sub-process during the MR of mirror-reversed letters (Alivisatos & Petrides, 1997; Ankaoua & Luria, 2022; Corballs & McMaster, 1996). According to this hypothesis, to fully canonicalize mirror-reversed letters, participants rotate these letters out of the plane (non-planar rotation) after their rotation in the plane (planar rotation), (Corballis & McMaster, 1996; Quan et al., 2017). It was argued that the presence of this additional process - labelled 'flip-over' – resulted in higher working memory (WM) loads on mirror-reversed compared to canonical letter trials which delayed RTs (Ankaoua & Luria, 2022).

Differences between the MR processes elicited by mirror-reversed and canonical letters have also been reported in event-related potentials (ERP) studies (Ankaoua & Luria, 2022; Hamm, Johnson & Corballis, 2004; Núñez-Peña & Aznar-Casanova, 2009; Quan et al., 2017). The rotation-related negativity (RRN) is an ERP component conceived as the psychophysiological correlate of the spatial transformation process in MRTs (for a review see Heil, 2002). The RRN component is elicited over parietal electrodes from around 350ms after the presentation of the stimulus and its amplitude is sensitive to the stimulus rotation angle, becoming more negative with increasing rotation angles (e.g., Heil & Rolke, 2002; Núñez-Peña & Aznar-Casanova, 2009; Núñez-Peña et al., 2005; Rösler et al., 1995; Wijers et al., 1989). A series of studies have shown the presence of the RRN for both canonical and mirror-reversed letters (Hamm et al., 2004; Zhao, Della Sala, Gherri, 2019a; 2019b; 2022). Hamm and colleagues (2004) first reported that the onset of the RRN was delayed on mirror-reversed compared to canonical letter trials. Núñez-Peña and Aznar-Casanova (2009) found that the modulation by rotation angle of the RRN amplitudes measured between 400-500ms was more evident during canonical than mirror-reversed letter rotation.

When ERPs elicited by upright canonical letters were subtracted from those elicited by upright mirror-reversed letters (i.e., in the absence of planar rotation), a negative-going waveform was observed between 400 and 500ms post-stimulus (Núñez-Peña and Aznar-Casanova, 2009). This increased negativity for mirror-reversed compared to canonical trials had a similar polarity and scalp distribution with respect to the RRN component which is considered the psychophysiological marker of planar rotation. Accordingly, it was suggested that the ERP differences between MR processes on canonical and mirror-reversed letter trials were due to the presence of the additional flip-over rotation (non-planar rotation) on mirror-reversed trials (Hamm et al., 2004; Núñez-Peña and Aznar-Casanova, 2009).

According to the 'flip-over' hypothesis, while participants perform both planar and non-planar rotation on mirror-reversed trials, they only complete a planar rotation on canonical letter trials. The RRN component on mirror-reversed trials is calculated through the subtraction of ERPs elicited by upright mirror letters from those elicited by rotated mirror letters. It was therefore suggested that the RRN in the mirror-reversed condition is at least in part cancelled out by the correlates of the non-planar 'flip-over' rotation which are present in the ERPs elicited by upright mirror-reversed condition when this is used as a baseline for the RRN calculation (Hamm et al., 2004; Núñez-Peña and Aznar-Casanova, 2009). Thus, the delay and reduced amplitude modulation by angle observed for the RRN on mirror-reversed compared to canonical letter trials have been interpreted as indirect evidence for the additional non-planar rotation.

One crucial information necessary to interpret these ERP data concerns the timing of the non-planar process relative to the planar one. The presence of the additional non-planar rotation on mirror-reversed letter trials compared to canonical ones can explain the RRN delay only if one assumes that the planar rotation begins at the same time for canonical and mirror-reversed letters and that this process overlaps temporally with the non-planar rotation on mirror-reversed trials. Although this assumption has been used to explain the delay in MR onset observed for mirror-reversed as compared to canonical letters (Hamm et al., 2004), it has not been fully tested. Differences between mirror-reversed and canonical trials (reflecting the non-planar rotation) are more likely to arise in the later phase of MR (Quan et al., 2017), occurring increasingly later as a function of the increasing rotation angles (Núñez-Peña and Aznar-Casanova, 2009). These observations have led researchers to suggest that the out-of-plane (non-planar) rotation occurs after planar rotation (Ankaoua & Luria, 2022; Núñez-Peña and Aznar-Casanova, 2009; Quan et al., 2017), allowing participants to fully canonicalize mirror-reversed letters after the planar rotation. However, because the difference between the RRN amplitudes elicited on canonical and mirror-reversed trials was absent for larger rotation angles (Núñez-Peña and Aznar-Casanova, 2009), it was further suggested that the non-planar rotation occurs sequentially after the planar rotation for smaller angles but in parallel for larger angles (Núñez-Peña and Aznar-Casanova, 2009; Quan et al., 2017). To the best of our knowledge, this temporal relationship between planar and non-planar rotation has not been tested statistically.

The aim of the present study was to investigate the time course of both planar and non-planar rotations during the MR of mirror-reversed letters. Based on previous literature (Núñez-Peña and Aznar-Casanova, 2009; Quan et al., 2017), we hypothesized that the non-planar rotation of mirror-reversed letters occurs at different times relative to their planar rotation for letters with different rotation angles. More specifically, we investigate whether the non-planar rotation occurs sequentially after the planar rotation for smaller rotation angles, whereas for larger angles these two processes occur in parallel.

2. Method

Participants

Forty-one paid participants were recruited from the University of Edinburgh. Ten participants had to be excluded because less than 50% trials remained after artefact rejection. Thus, the performance of 31 participants (15 women), between 18 and 28 years of age (mean = 22.3 ± 0.9 years old) was considered for data analyses. All participants were right-handed and had canonical or corrected-to-canonical vision. Informed consent was formally obtained. All study procedures were approved by the Psychology Committee, University of Edinburgh and the research was carried out in compliance with the declaration of Helsinki.

Stimuli and Experimental procedure

Participants were seated in an electrically shielded, dimly lit, sound attenuating room. The computer monitor was located at a distance of 76 cm in front of the participants, whose eyes were aligned with the monitor centre. Upper character letters (F, L, P and R) were used as stimuli in this study (in line with existing ERP studies of letter MR, c.f. Heil, 2002; Heil, & Rolke, 2002; Núñez-Peña & Aznar-Casanova, 2009). The letters were presented in white on a black background (height: 3 cm, 2.26° of visual angle). These letters were presented in a canonical mode (normal letter) or flipped according to their vertical meridian (mirror letter). On different trials these stimuli were presented at different orientations with a rotation angle of 0°, 30°, 60°, 90°, 120° and 150° (six rotation angles)(Fig.1A). Stimulus rotation followed two different directions clockwise or counter-clockwise from the vertical upright position of the stimuli.

As shown in Figure 1B, each trial began with a white fixation cross (1cm × 1cm) presented at the centre of a black background for 100ms. This was followed by a letter presented at the screen centre for 500ms, after which a fixation cross remained on the screen for a variable interval randomly selected between 1,800 and 2,100ms. Participants were instructed to respond as fast and as accurately as possible to determine whether the letter on the screen was presented as normal or mirrored version. Each block included 96 trials (4 letters × 2 stimulus types × 6 rotation angles × 2 rotation symmetry) presented in random order. Each participant completed ten blocks.

------ insert Figure 1 about here-------

During the EEG recording, participants were instructed to keep their eyes on the fixation cross and their index fingers on the two keys on the response box, which was vertically arranged in front of them. The top key was set for responses to normal stimuli and the bottom key was set for responses to mirror stimuli. While the stimulus to response key mapping was held constant throughout the experiment, the responding hand to response key mapping (left hand on the top key and right hand on the bottom key) was changed after each block. Before the experiment began, participants completed a training block of 48 trials to familiarise with this MRTs. Here, the letters "G" and "J" were used which were not included in the set of experimental stimuli.

EEG Recording and Pre-processing

EEG was recorded from 70 active electrodes (BioSemi Active Two system). Horizontal EOG (hEOG) was recorded unipolarly from the outer canthi of both eyes and vertical EOG (vEOG) was recorded bipolarly both vertically from above and below the right eye. The impedances of the earlobe reference electrodes were kept as equal as possible. The digitisation rate was 512 Hz. We used BrainVision Analyzer 2.0 (BrainVision Analyzer, Version 2.2.2, Brain Products GmbH, Gilching, Germany) to complete EEG pre-processing. EEG was digitally re-referenced to the average of the left and right earlobe and was digitally filtered offline (high-pass filter 0.53 Hz, low-pass filter 40 Hz and notch filter 50 Hz). EEG, hEOG and vEOG were segmented into 750ms long epochs starting from 100ms before stimulus onset. Trials with eye blinks (VEOG exceeding $\pm$ 60 μV), horizontal eye movements (HEOG exceeding $\pm$ 80 μV), or other artefacts (a voltage at any scalp site exceeding $\pm$ 80 μV) throughout the epoch were excluded from analysis. Only epochs recorded on correct trials were included in the ERP analyses. ERPs recorded on these trials were averaged relative to a 100 ms pre-stimulus baseline separately for each rotation angle on canonical (average number of trials per rotation angle, M = 70.99, SD= 6.31) and mirror-reversed letter trials (average number of trials per rotation angle, M= 71.54, SD= 5.85).

Data Analysis

Behavioural Analysis

Two repeated-measures analyses of variance (ANOVA) were performed on accuracy rates and on correct response times averages (RTs) which included rotation angle (0°, 30°, 60°, 90°, 120°, 150°)[1] and stimulus type (canonical or mirror-reversed) as within-subjects factors. The Greenhouse-Geisser correction for sphericity violation was applied when appropriate. Simple effect tests were performed in the presence of a significant interaction. Orthogonal polynomial contrasts were conducted to discover the linear or quadratic trends of variables.

General ERPs Analysis

To make sure results of the present study were in line with the existing literature, a first ERPs analysis was to explore the presence of mental rotation effort in both canonical and mirror-reserved letters. The RRN component was calculated by subtracting the ERPs elicited by rotated letters from ERPs elicited by upright letters between 400 and 600ms post stimulus onset based on visual inspection of the ERP waveforms and consistently with existing literature (c.f. Heil, 2002; Quin et). This repeated-measure ANOVA included rotation angle (0°, 30°, 60°, 90°, 120°, 150°) and stimulus type (canonical *vs.* mirror-reversed letters) as within subject factors. Greenhouse-Geisser corrections for sphericity violations were applied when appropriate. The presence of significant rotation angle×stimulus type interactions were followed up by orthogonal polynomial contrasts carried out separately for each stimulus type to investigate whether the amplitude of the RRN component increased linearly with increasing rotation angles.

Separate ERPs Analysis by Rotation Angle

The crucial question of the present study was assessed through a second ERPs analysis, similar to that described in the Núñez-Peña and Aznar-Casanova's study (2009). ERPs mean amplitudes were computed for successive 50ms-interval separately

[1] Preliminary analyses were performed on behavioural and EEG data to test rotation symmetry (clockwise *vs.* counter-clockwise). No asymmetries were detected and the data were collapsed across clockwise and counter-clockwise into six rotation angles (0°, 30°, 60°, 90°, 120°, 150°).

for each rotation angle and each stimulus type from 300 to 850ms post-stimuli collapsed across ten electrodes (CP1/2, CP3/4, P1/2, P3/4, CPz, Pz). The factor laterality was not taken into account because the difference between ERPs on canonical and mirror-reversed trials was centrally distributed, being larger over central (CPz and Pz) as compared to lateral electrodes on the left (CP3, P3) or right hemisphere (CP4, P4) as revealed by preliminary analyses[2].

To investigate the temporal relationship between planar and non-planar rotation, separate ANOVAs were conducted for each rotation angle and for each of the consecutive 50ms-intervals from 300 to 850ms post-stimulus. These repeated-measures ANOVAs included the factors stimulus type (canonical *vs.* mirror-reversed) and rotation angles (0° *vs.* rotated angle X°) as within-subjects factors and were carried out on the ERPs mean amplitudes computed separately for each rotation angle (30°, 60°, 90°, 120°, 150°) at central-parietal sites (CP1/2, CP3/4, P1/2, P3/4, CPz, Pz). In these analyses, main effects of rotation angle (significant difference between ERPs measured for 0° and X° rotation angles) reflected the presence of *planar rotation* (enhanced negativity for rotated than upright letters) as indexed by the presence of a significant RRN component. The main effect of stimulus type (more negative ERP amplitudes for mirror-reversed than canonical letters) reflected the presence of *non-planar rotation* processes. We were specifically interested in post-hoc comparisons exploring the statistical presence of *planar rotation* (rotation angle simple effects) for each stimulus type as well as the presence of *non-planar rotation* (simple effects of stimulus type) for each rotation angle. Bonferroni corrections were applied whenever appropriate. Greenhouse-Geisser corrections were used in case of sphericity violations. Partial η^2-

[2] Preliminary ERP analyses included the factor laterality (left- vs. central vs. right- parietal sites, pooled over CP3 and P3, CPz and Pz, and CP4 and P4, respectively). Main effects of laterality emerged to be significant in all the 50ms-intervals time windows measured between 300 and 1000ms, all Fs ≥ 3.96, ps $\leq .024$, $\eta^2 \geq .12$, with larger ERP amplitudes at central as compared to left or right sites. However, there was no interaction involving the factor laterality in any of the time windows considered, all p-values$>.05$.

values for each significant main effects or interactions were reported as well as the corrected *p*-values.

3. Results

Behavioural Results

Accuracy rates

Results revealed a main effect of stimulus type, F (1, 30) = 4.76, p = .037, η^2 = .14 (canonical letters, M = 93.7%, SE = 0.8; mirror-reversed letters, M = 95.1%, SE = 0.7). There was also a main effect of rotation angle, F (1.6, 46.9) = 32.96, p < .001, η^2 = .52, revealing that the accuracy rates linearly decreased with increasing rotation angles, F (1, 30) = 40.26, p < .001, η^2 = .57. As shown in the left panel of Figure 2, there was a significant interaction between stimulus type and rotation angle, F (1.9, 57.1) = 13.5, p < .001, η^2 = .31. The main effect of rotation angle was present for both canonical (F (1.6, 47.6) = 31.72, p < .001, η^2 = .51) and mirror-reversed letters (F (1.9, 56.4) = 7.27, p = .002, η^2 = 20). To explore the interaction further direct contrasts between canonical and mirror-reversed trials were carried out for each rotation angle. No significant difference was present between canonical and mirror-reversed accuracy rates for 0°, 60°, and 90° (all *t*s (31) ≤ 1.78, *p*s≥.086). For 30°, responses were more accurate on canonical than mirror-reversed letter trials (t (31) = 2.50, p=.018), whereas for larger rotation angles responses were less accurate for canonical than mirror-reverse letters (120°: t (31) = -2.11, p=.043; 150°: t (31) = -4.48, p<.001).

------insert Figure 2 about here ------

Response times

Consistent with the existing literature, RTs were significantly longer for mirror-reversed (M = 698.29ms, SE = 21.17) than canonical letters (M = 621.43ms, SE = 17.36), F (1, 30) = 63.53, p < .001, η^2 = .68. As shown in Figure 2 (right panel), the RT analysis revealed a main effect of rotation angle, F (1.7, 49.6) = 209.7, p < .001,

η^2 = .88, with longer RTs for increasing rotation angles. The trend analysis revealed that RTs were described by both a linear, F (1, 30) = 291.74, p < .001, η^2 = .91, and a quadratic trend, F (1, 30) = 63.07, p < .001, η^2 = .68.

In addition, results revealed a significant interaction between rotation angle and stimulus type, F (2.7, 80.8) = 2.88, p = .046 η^2 = .09. Separate analyses carried out for canonical and mirror-reversed letters showed that the main effect of rotation angle was reliably present for both types of stimuli, both Fs ≥ 113.52, ps < .001, η^2 ≥ .79. For both canonical and mirror-reversed letters, the RTs function departed from linearity (both Fs ≥184.69, ps < .001, η^2 ≥ .86) and contained a quadratic component (both Fs ≥ 23.12, ps < .001, η^2 ≥ .44).

Electrophysiological Results

General analysis

To make sure that results of the present study were comparable to those already reported in the literature, a general ANOVA was carried out on RRN component (the ERP difference waveforms subtracted ERPs amplitudes in each rotated angles from ERPs amplitudes in upright position respectively) to demonstrate that for both canonical and mirror-reversed letter trials ERP amplitudes were increasingly negative for increasing rotation angles. To this aim one single time window 400-600ms was considered (c.f., Heil, 2018; Quan et al., 2017) with rotation angle and stimulus type as within subject factor. As shown in Figure 3, results revealed the presence of a rotation angle main effect, a stimulus type main effect as well as the rotation angle by stimulus type interaction (all Fs ≥5.18, ps <.001). Post-hoc analyses revealed significant main effects of rotation angle in both canonical (F (5, 150) = 31.06, p<.001, η^2 = .51) and mirror-reversed letter trials (F (5, 150) = 29.98, p <.001, η^2 = .50). In both cases, increasingly negative ERPs amplitudes emerged for progressively larger rotation angles (both Fs (1, 30) ≥57.54, ps <.001, η^2 ≥.66).

------insert Figure 3 about here ------

Separate analyses by rotation angle

Our primary interest in this experiment was the time course of planar and non-planar rotations and their possible interactions for each rotation angle. To investigate the statistical presence of the effects of planar and non-planar rotation, ANOVAs with stimulus type (canonical vs. mirror-reversed letters) and rotation angle (upright vs. rotation angle), were carried out separately for consecutive 50 ms time-windows between 300 and 850 ms post-stimulus and for each rotation angle (> 0°). A summary of the main results is reported separately for each rotation angle in Table 1 (30°), Table 2 (60°), Table 3 (90°), Table 4 (120°), and Table 5 (150°). ERPs amplitudes that were more negative on rotated than upright letter trials (planar rotation) and more negative on mirror-reversed than canonical letter trials (non-planar rotation) are marked with a black box and a grey background.

ERPs elicited by canonical (C) and mirror-reversed (M) letters at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) are shown separately for each rotation angle in Figure 3 (30°), Figure 4 (60°), Figure 5 (90°), Figure 6 (120°), and Figure 7 (150°). The bottom left panels (Panel B) show the ERPs mean amplitudes elicited by rotated (dotted line) and upright letters (solid line) and by canonical (C, black) and mirror-reversed letters (M, grey). In these panels, the time windows in which significant interactions between rotation angle and stimulus type were present (see Tables 1-5) were marked with a red dotted box. In the bottom right panels (Panel C), the ERP difference waveforms between rotated and upright letters is shown separately for canonical (Planar MR for C, black solid line) and mirror-reversed trials (Planar MR for M, grey solid line). Difference waveforms between mirror-reversed and canonical letters (non-Planar MR for M, grey dotted line) were also shown separately for each rotation angle. The top panels (Panel A) in these figures show the scalp distribution of the corresponding difference waveforms between ERPs elicited at pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) by upright and rotated letters for canonical (Planar MR for C, C0° vs. CX°) and mirror-reversed letters (Planar MR for M, M0° vs. MX°) as well as between mirror-reversed and canonical letters (non-Planar

MR for M, MX° vs. CX°) in successive 50ms time windows from 300 to 850ms post-stimulus. Intervals with significant effects of rotation angle for each angle were marked with black solid frame.

As shown in Figures 3-7, systematic differences emerged between the effect of planar rotation for mirror-reversed as compared to canonical trials. By and large, a delayed planar rotation process can be observed for mirror-reversed compared to canonical letters (with the exceptions of 30° rotation angle - in which planar rotation is absent on canonical letter trials - and of 150° - in which the planar rotation process emerges at the same time for canonical and mirror-reversed letters). Crucially, during the processing of mirror reversed letters, the relative timing of planar and non-planar rotation processes differed between rotation angles. For smaller angles (30° and 60°, see black box in Fig.2 and 3, respectively), non-planar rotation emerged earlier than planar rotation. For the 90° rotation angle, planar and non-planar rotation emerged approximately at the same time (around 400-450ms, see black box in Fig.4), whereas for larger rotation angles (120° and 150°, black box in Fig.5 and 6, respectively), planar rotation emerged earlier than non-planar rotation.

30° rotation angles

For the 30° rotation angle, main effects of rotation angle were present in the 300-350ms time window (F= 4.6, p =.040, η^2 =.13), reflecting more negative ERP amplitudes for rotated (30°) than upright letters in this interval. Main effects of stimulus type emerged between 300 and 500ms with enhanced negativities for mirror-reversed than canonical letters (all Fs≥8.2, ps≤.008, η^2≥.21).

Rotation angle interacted with stimulus type (Fig.4B) in the time windows between 400 and 600ms (all Fs≥6.0, ps≤.020, η^2≥.17). Follow-up comparisons were conducted separately for canonical and mirror-reversed letters to explore effects of rotation angle (0° vs. 30°, planar rotation, Table 1), and for 30° rotation angle letters to explore the presence of the effect of stimulus type (canonical vs. mirror-reversed, non-planar rotation, Table 1). As shown in Figure 4, panels B and C, no effect of rotation angle (planar rotation for C) was present for canonical letters. On mirror-reversed trials, the presence of rotation angle effects (planar rotation for M) was evident between 500 and 600ms post-stimulus while stimulus type effect (non-planar rotation for M) emerged between 300 and 500ms with more negative ERP amplitudes in mirror-reversed than canonical letters.

------insert Figure 4 about here ------

------insert Table 1 about here ------

60° rotation angles

For letters rotated by 60°, main effects of rotation angle (350-500ms; all *F*s≥5.2, *p*s ≤.031, η^2 ≥.15) reflected more negative ERP amplitudes for rotated than upright letters. Between 300-500ms, the main effects of stimulus type revealed that ERP amplitudes were more negative for mirror-reversed than canonical letters (all *F*s≥5.5, *p*s ≤.026, η^2 ≥.15).

In addition, significant interactions between stimulus type and rotation angle were present between 450 and 700ms (see bottom left panel in Fig.5), all Fs≥5.2, ps ≤.031, η2≥.15. Follow-up comparisons were conducted separately for canonical and mirror-reversed letters to explore effects of rotation angle (0° vs. 60°, planar rotation, Table 1), and for 60° rotation angle letters to explore the presence of the effect of stimulus type (canonical vs. mirror-reversed, non-planar rotation, Table 2). As shown in Panels B and C of Fig.5, a rotation angle effect (planar rotation for C) was evident between 350 and 400ms post-stimulus onset for canonical letters with more negative ERPs for rotated (60°) than upright letters. For mirror-reversed letters, effect of rotation angle (planar rotation for M) was present between 400 and 650ms. In this interval, ERPs elicited by mirror-reversed letters were more negative for rotated (60°) than upright letters. The effect of stimulus type (non-planar rotation for M) was observed between 350 and 500ms with more negative ERPs amplitudes elicited in mirror-reversed than canonical letters. Thus, for mirror-reversed letters the non-planar rotation emerged earlier than the planar rotation.

------insert Figure 5 about here ------

------insert Table 2 about here ------

90° rotation angles

For the 90° rotation angle, rotation angle main effects were obtained in the intervals between 300 and 550ms (all *F*s ⩾ 5.3, *p*s ⩽ .029, η^2 ⩾ .15) with ERP amplitudes more negative for rotated (90°) than upright letters. Main effects of stimulus type were obtained between 350 and 500ms (all *F*s≥6.2, *p*s ≤.015, η^2 ≥.18). In this interval, ERP amplitudes were more negative for mirror-reversed than canonical letters.

As depicted in Fig.6 Panel B, stimulus type interacted with rotation angle between 300 and 350ms (all *F*s =5.3, *p*s =.029, η2 =.15) and between 450 and 700ms (all Fs≥6.6, ps ≤.015, η2 ≥.18). Follow-up analyses were conducted separately for each stimulus type (see Table 3). ERPs elicited by canonical letters were more negative for rotated (90°) than upright letters (planar rotation for C) between 300 and 500ms. For mirror-reversed letters, rotation angle effects (planar rotation for M) emerged between 400 and 650ms with more negative ERPs for rotated (90°) than upright letters. The stimulus type effects (non-planar rotation for M) were present in three consecutive time windows between 400 and 550ms. In these time windows, ERP amplitudes were significantly more negative for mirror-reversed than canonical letters. Thus, for mirror-reversed letters both planar and non-planar rotation processes were significantly present between 400 and 450 ms, although planar rotation lasted longer.

------insert Figure 6 about here ------

------insert Table 3 about here ------

120° rotation angles

For letters rotated by 120°, rotation angle main effects were present between 350 and 600ms (all *F*s≥5.8, *p*s ≤.022, η^2 ≥.16) with ERP amplitudes more negative for rotated (120°) than upright letters. Main effects of stimulus type were observed between 400 and 500ms (both *F*s≥4.3, *p*s ≤.046, η^2 ≥.12) with more negative ERP amplitudes for mirror-reversed than canonical letters.

As shown in Fig.7, Panels B and C, the interactions between stimulus type and rotation angle were significant between 300 and 450ms (all Fs≥8.3, ps ≤.007, η^2 ≥.22) and between 500 and 800ms post stimulus (all Fs≥4.3, ps ≤.047, η^2 ≥.13). Follow-up analyses were conducted separately for each stimulus type (Table 4). As can be seen in Fig.7, effects of rotation angle for canonical letters (Planar rotation for C) were present between 300 and 500ms with more negative ERP amplitudes for rotated (120°) than upright canonical letters. For mirror-reversed letters, rotation angle effects (Planar rotation for M) were obtained between 400 and 650ms post-stimulus, with more negative ERP amplitudes observed for rotated (120°) than upright mirror-reversed letters. The presence of stimulus type effects (non-Planar rotation) emerged between 550 and 650ms. ERP elicited by mirror-reversed letters were more negative compared to canonical letters in this interval. For mirror-reversed letters rotated by 120°, planar rotation emerged earlier than non-planar rotation, see Fig.7.

------insert Figure 7 about here ------

------insert Table 4 about here ------

150° rotation angles

For letters rotated by 150°, both rotation angles (350-650ms: all Fs≥6.3, ps ≤.018, η^2 ≥.17) and stimulus type simple effects (350-450ms: both Fs≥5.0, ps ≤.033, η^2 ≥.14) were obtained. The rotation angle main effects between 350 and 650ms reflected the fact that ERP amplitudes were more negative for rotated (150°) than upright letters. In addition, the presence of stimulus type main effect between 350 and 450ms post-stimulus with more negative ERP amplitudes observed for mirror-reversed than canonical letters.

Interactions between rotation angle and stimulus type were significant between 350 and 450ms (both Fs≥4.6, ps ≤.041, η2 ≥.13) and between 550 and 950ms post-stimulus (all Fs≥4.5, ps ≤.042, η^2 ≥.13)(see the red dotted frame in Fig.8B). As shown in Table 5 and Fig.8, follow-up analyses showed the presence of significant simple effects of rotation angle for both canonical (Planar rotation for C, 300-550ms) and mirror-reversed letter trials (Planar rotation for M, 350-700ms) with more negative ERP amplitudes for rotated (150°) than upright letters. Follow-up analyses were also carried out separately for letters rotated by 150°. Stimulus type effects (non-Planar rotation for M) were significantly present between 600 and 850ms with more negative ERP amplitudes observed for mirror-reversed than canonical letters. For mirror-reversed letters rotated by 150°, planar rotation emerged before non-planar rotation.

------insert Figure 8 about here ------

------insert Table 5 about here ------

4. Discussion

In the present study a letter MRT was used to investigate the differences between the MR processes engaged during the rotation of canonical and mirror-reversed letters. Overall, the pattern of results observed replicated the widely documented canonical-mirror-reversed difference for both behavioural (e.g., Cooper & Shepard, 1973; Kung & Hamm, 2010) and ERP measures (Hamm et al., 2004; Zhao, et al., 2019a; 2019b). For both canonical and mirror letters, RTs linearly increased as a function of rotation angles, although RTs on canonical letter trials could also be described by a quadratic trend. Across different rotation angles, longer RTs were recorded on mirror-reversed than canonical letter trials, suggesting that the categorization of the letter took longer for mirror-reversed than canonical stimuli. Accuracy rates linearly decreased with increasing rotation angles for both canonical and mirror-reversed letter trials (e.g., Hamm et al., 2004; Núñez-Peña and Aznar-Casanova, 2009). For 30° rotation angles, responses were more accurate on canonical than mirror-reversed letter trials, whereas for larger rotation angles (120° and 150°), more errors were observed in canonical than in mirror-reversed letter trials. This latter observation is in line with previous studies in which stimuli were presented on the screen for a limited period of time (500 ms; e.g., Núñez-Peña and Aznar-Casanova, 2009). Considering the relatively short letter representation time in the present study, this could be accounted for by posing a different representation between the two sets of stimuli (Ankaoua & Luria, 2022). Participants might have had difficulties accessing the perceptual information after stimulus offset in canonical trials, whereas they were more able to rely on its internal representation in mirror letter trials. It is relevant to note that the cognitive process of planar and non-planar rotation for mirror-reversed stimuli can only be observed for certain familiar, asymmetrical stimuli (e. g., character letters). The results of the present study may not be applicable to other types of MR tasks with different stimuli and/or task requirements (c.f.,Vergara-Martínez, Gomez, Perea, 2020).

The current results revealed significant differences between ERPs elicited by upright and rotated letters reflecting the process of planar rotation. In line with existing evidence, ERP waveforms became more negative as a function of the increasing rotation angles (Heil, Rauch, & Hennighausen, 1998; Heil & Rolk, 2002). Importantly, this correlate of *planar rotation* was significantly present for both canonical and mirror-reversed letters (Fig.4-8, Panel A), though with relevant differences. The time course of planar rotation in mirror-reversed letters was delayed as compared to canonical ones especially for larger angles (90° and 120°), which is in line with previous observations (Hamm et al., 2004; Milivojevic, Hamm & Corballis, 2011).

To fully canonicalize mirror-reversed letters participants rotate the letter not only within the plane (planar rotation) but also out-of-the plane (non-planar rotation). The presence of the *non-planar rotation* processes (flip-over) was revealed by the direct comparisons between ERPs elicited on canonical and mirror-reversed letter trials for any given rotation angle. The corresponding difference waveforms reflecting the correlate of non-planar rotation (difference between ERPs on mirror-reversed and canonical trials) were statistically present for all rotation angles and characterized by a negative-going deflection (grey dotted line, Fig.4-8, Panel C) in line with results described in previous ERP studies (Hamm et al., 2004; Núñez-Peña & Aznar-Casanova, 2009). Importantly, the correlate of non-planar rotation was observed progressively later for increasing rotation angles.

The aim of the present study was to test the hypothesis that the non-planar rotation of mirror-reversed letters occurs after their planar rotation is completed. To address this, we explored systematically the temporal relationship of the two mental rotation processes elicited on mirror-reversed trials: 1) *planar rotation* (the difference between rotated and upright letter trials, e.g., Mx° – M0°) and 2) *non-planar rotation* (the difference between mirror-reversed and canonical letter trials for any given rotation angle, e.g., Mx° – Cx°).

The direct comparison of the time course of planar and non-planar rotation for mirror-reversed letters revealed that these rotation processes were engaged at different times for different rotation angles. Specifically, for 30° mirror-reversed letters (Fig.4 and Tables 1), the process of non-planar rotation preceded that of planar rotation with little temporal overlap (non-planar rotation was reliably present between 300-500ms whereas planar rotation was observed between 500-650ms). Similarly, for 60° (Fig.5 and Table 2), non-planar rotation emerged earlier than planar rotation, although there was temporal overlap between these processes between 400 and 550 ms post-stimulus (non-planar rotation was observed between 350 and 550ms while planar rotation was present between 400 and 650ms). For 90° (Fig.6 and Table 3), planar and non-planar rotations occurred in parallel, being simultaneously present between 400-450ms post stimulus onset. For relatively larger rotation angles (120° and 150°, Fig.7 and 8, Table 4 and 5), planar rotation emerged earlier than non-planar rotation (planar rotation between 400 and 650ms for 120° and 350-700 ms for 150°; non-planar rotation was present between 500-650ms post-stimulus for 120° and between 600 and 850ms for 150°).

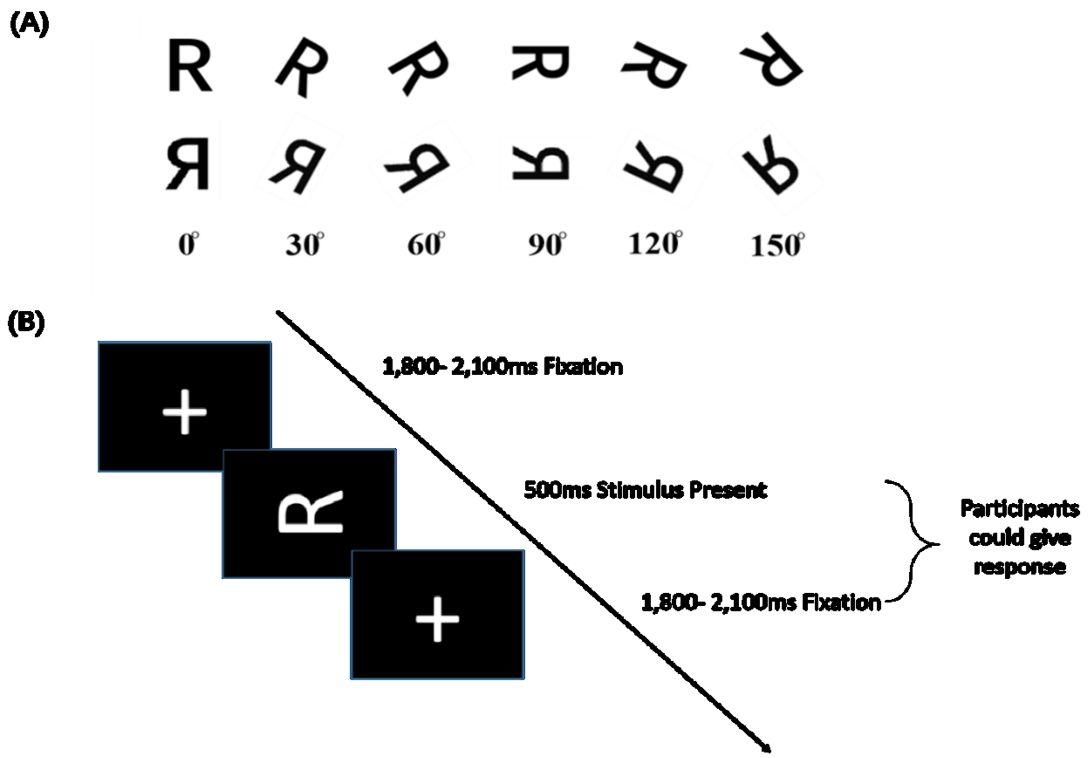
Previous studies have suggested that the non-planar rotation occurs after the planar rotation for smaller angles, but these processes are elicited in parallel for larger rotation angles (Núñez-Peña & Aznar-Casanova, 2009; Quan et al., 2017). Results of the present study demonstrated a different pattern of results with the relative time course of planar and non-planar rotation entirely depending on the rotation angle of the mirror-reversed letter. While for mirror-reversed letters with smaller rotation angles (30°, 60°), non-planar rotation emerged before the planar rotation, the opposite was true for larger rotation angles (120° and 150°). For intermediate angles (90°), both rotation processes emerged in the same time windows, occurring in parallel. These findings are particularly interesting because the possibility that the non-planar rotation was engaged before the planar one had been previously discounted based on logical grounds (i.e., if participants first rotate the letter out-of-the-plane, they know already they are mentally manipulating a mirror letter, and it is no longer necessary to rotate this within the plane).

Although participants are unlikely to prepare a canonical letter response on all trials (c.f. Cooper and Shepard, 1973), we suggest that they are able to form a working hypothesis about the parity of the letter upon stimulus presentation. This hypothesis which is characterised by a higher or lower level of confidence based on the stimulus type and the rotation angle, is then tested through planar and/or non-planar rotation processes. For smaller rotation angles, participants are immediately able to determine whether the letter is canonical (no planar rotation is observed for smaller angles in canonical condition). Thus, if the letter is not canonical, they can hypothesize that they are dealing with a mirror-reversed letter. This hypothesis is tested first through an out-of-the-plane (non-planar) rotation (i.e., 30°mirror-reversed letters). If this is not sufficient, participants will then rotate the letter representation within the plane planar rotation), to fully canonicalize it (i.e., 60°mirror-reversed letters). Thus, although the planar rotation is not strictly necessary, it is performed after the non-planar rotation simply to increase participants' confidence in the hypothesis that they are dealing with a mirror letter. As the mental demands of the planar rotation are increased (with increasing rotation angles), participants become increasingly uncertain about their initial hypotheses relative to the identity of the letter. Consequently, they tend to process both canonical and mirror-reversed letters in a similar manner by first applying a planar rotation. If by the end of the planar rotation the letter is not fully canonicalized, they will further perform the non-planar rotation, to verify that they are rotating a mirror-reversed letter.

Most neuroimaging studies so far have investigated the brain structures activated during *planar rotation,* consistently reporting brain activity in posterior brain regions (for review see Zacks, 2008). These include the early visual cortex - involved in the generation and maintenance of the mental representation of the stimulus (Albers, et al., 2013; Christophel et al., 2015) – and the parietal lobes - classically associated with the planar rotation of the stimulus in participants' minds (e.g., Thérien et al., 2022; Zacks, 2008). Notably, however, little is known about the brain structures that mediate the process of non-planar rotation. Some authors have suggested that both planar and non-planar rotation processes are implemented by the same neural structures based on the similar scalp distributions observed in ERP studies (Hamm et al., 2004). In line with this, also informal observation of our data appears to confirm the presence of similar scalp distributions for the correlates of planar and non-planar rotation. However, the finding that both these rotation processes can occur in parallel may suggest that the underlying brain structures are at least in part independent. Because the ERP methodology is not well suited to address questions related to the spatial nature of brain activity, future neuroimaging studies should directly investigate the question of the brain structures underlying planar and non-planar MR processes.

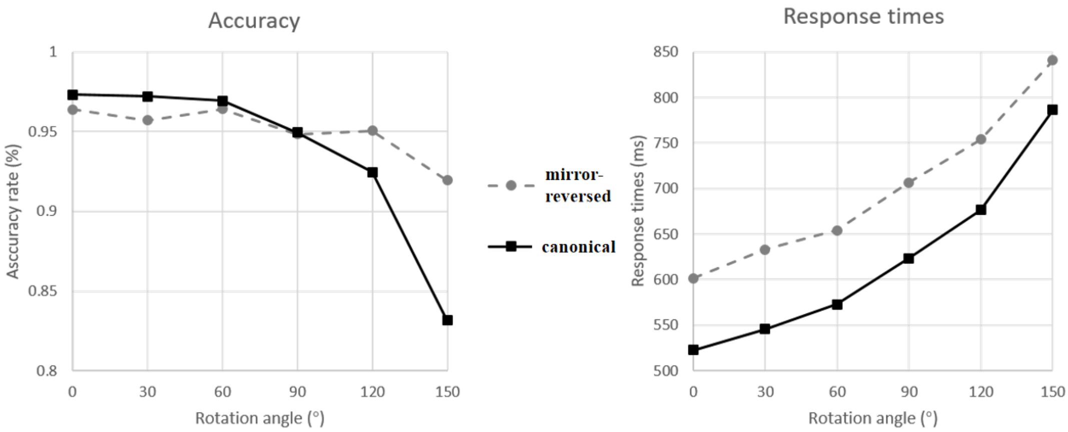
The finding that the non-planar rotation occurs at different points in time for different rotation angles has relevant consequences for the study and interpretation of MR processes elicited during a letter rotation task. As first suggested by Hamm and colleagues (2004) computing the RRN component for mirror-reversed letters using the ERPs elicited on upright mirror-reversed letter trials as a baseline can distort the data. Because the non-planar rotation is engaged much earlier for upright than for rotated mirror-reversed letters, its subtractions from rotated ERPs will result in the subtraction of part of the planar rotation process instead. Indeed, a better option is to use the ERPs elicited by upright canonical letter as a baseline for the mirror-reversed letter RRN. However, by doing do it is relevant to remember that both planar and non-planar rotation processes will be present in the mirror-reversed RRN. In other words, it is a methodological challenge to disentangle the processes of planar and non-planar rotation elicited during the MR of mirror-reversed letters. Depending on the specific research question, researchers may decide to analyse the raw ERP data (as shown in the present study) rather than the subtracted waveforms reflecting the RRN component when investigating the MR engaged for mirror-reversed letters in this specific MRTs.

Figure 1



(A)
0°
30°
60°
90°
120°
150°
(B)
1,800- 2,100ms Fixation
500ms Stimulus Present
1,800- 2,100ms Fixation
Participants could give response

Figure 2



Accuracy
1
0.95
0.9
0.85
0.8
Asccuracy rate (%)
0
30
60
90
120
150
Rotation angle (°)
mirror-
reversed
canonical
Response times
850
800
750
700
650
600
550
500
Response times (ms)
0
30
60
90
120
150
Rotation angle (°)

Figure 3

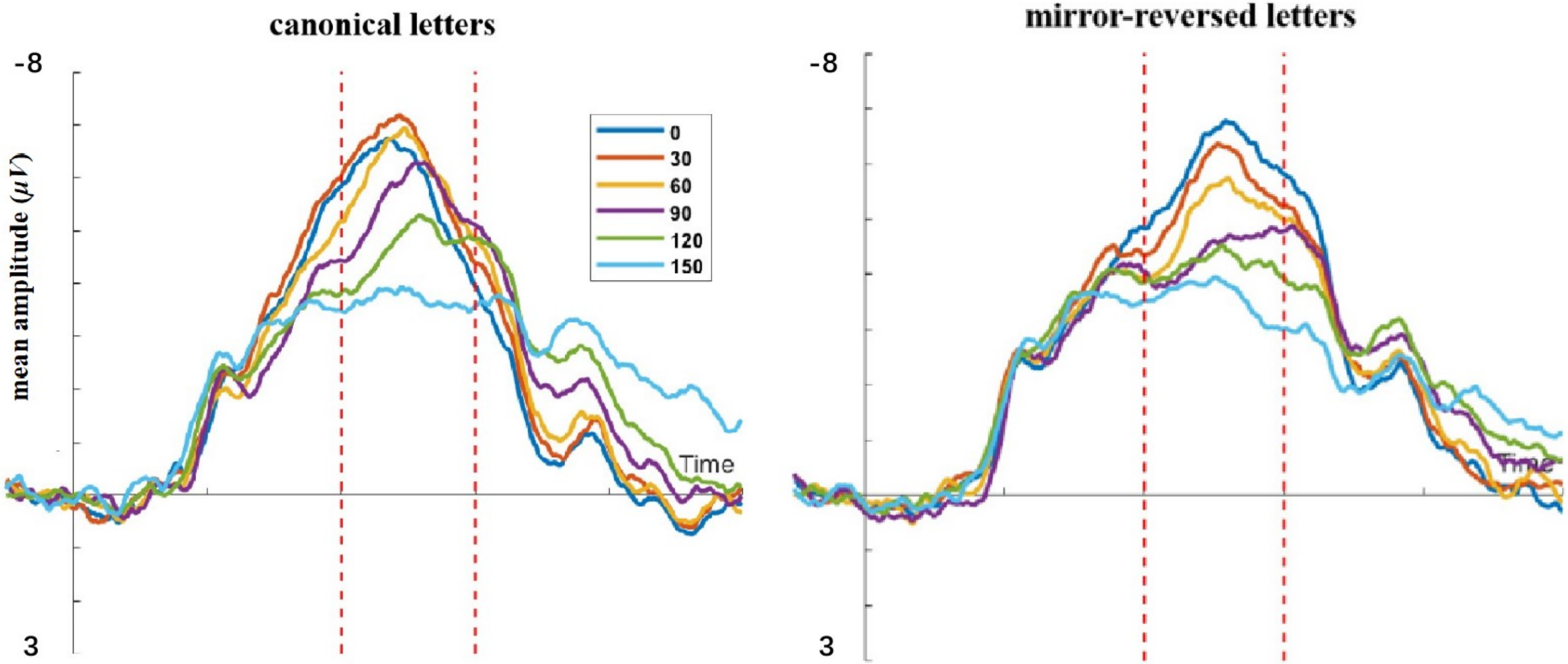

canonical letters
mirror-reversed letters
-8
-8
mean amplitude (μV)
0
30
60
90
120
150
Time
Time
3
3

Figure 4

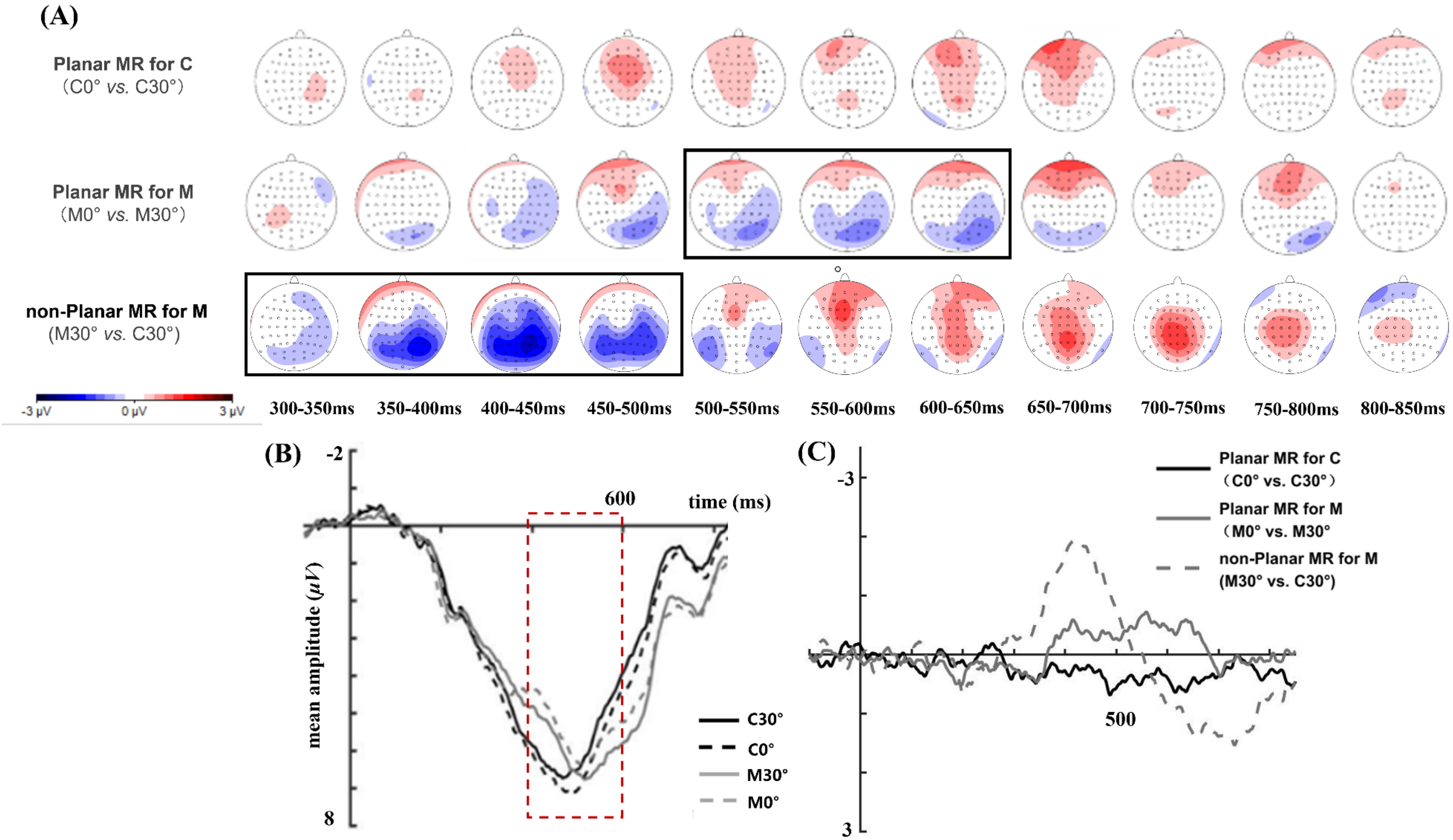
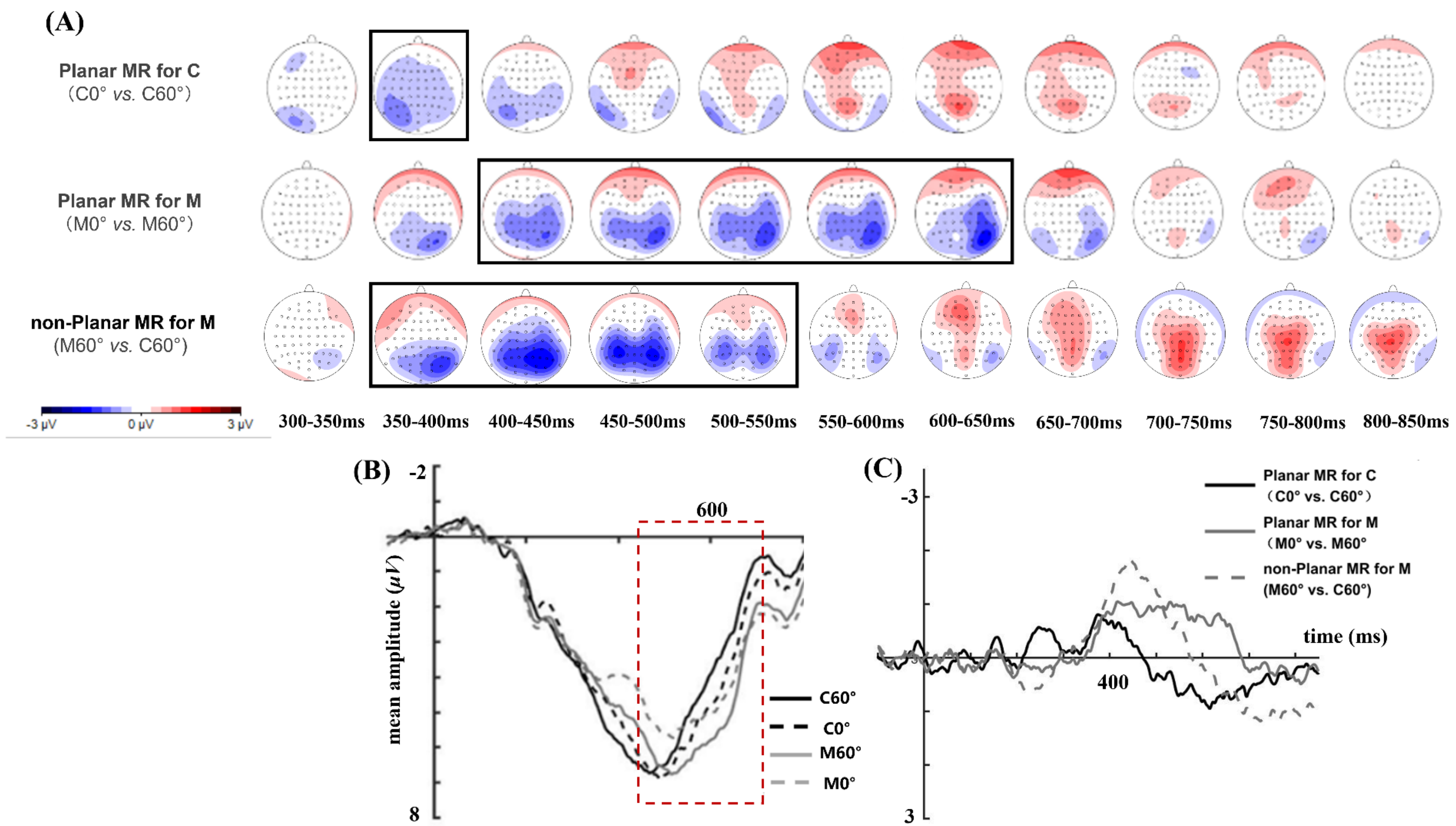
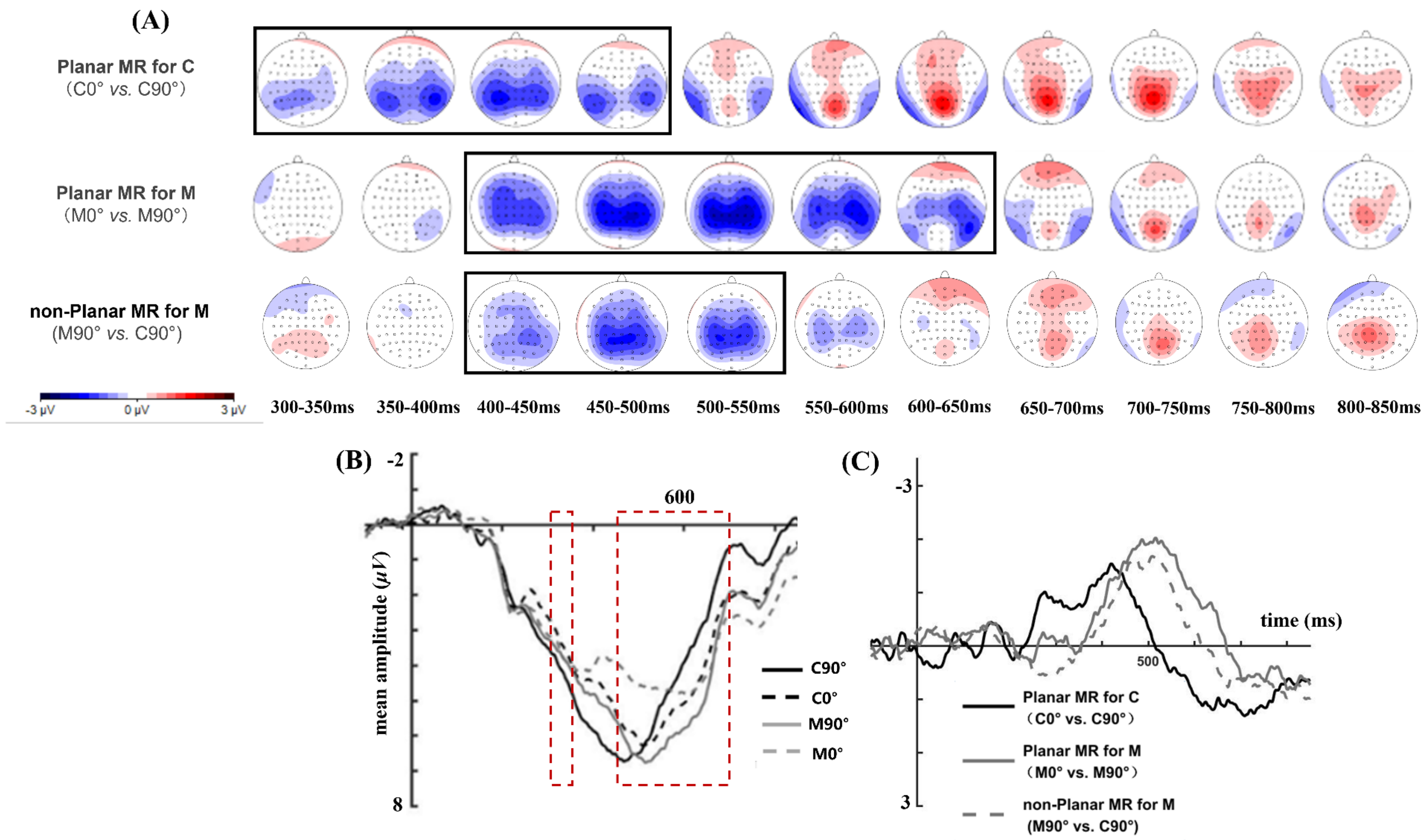

(A)
Planar MR for C
（C0° vs. C30°）
Planar MR for M
（M0° vs. M30°）
non-Planar MR for M
(M30° vs. C30°)
-3 µV
0 µV
3 µV
300-350ms
350-400ms
400-450ms
450-500ms
500-550ms
550-600ms
600-650ms
650-700ms
700-750ms
750-800ms
800-850ms
(B)
-2
8
600
time (ms)
mean amplitude (µV)
C30°
C0°
M30°
M0°
(C)
-3
3
500
Planar MR for C
（C0° vs. C30°）
Planar MR for M
（M0° vs. M30°
non-Planar MR for M
(M30° vs. C30°)

Figure 5



(A)
Planar MR for C
(C0° vs. C60°)
Planar MR for M
(M0° vs. M60°)
non-Planar MR for M
(M60° vs. C60°)
-3 µV
0 µV
3 µV
300-350ms
350-400ms
400-450ms
450-500ms
500-550ms
550-600ms
600-650ms
650-700ms
700-750ms
750-800ms
800-850ms
(B)
-2
8
600
mean amplitude (µV)
C60°
C0°
M60°
M0°
(C)
-3
3
400
time (ms)
Planar MR for C
(C0° vs. C60°)
Planar MR for M
(M0° vs. M60°
non-Planar MR for M
(M60° vs. C60°)

Figure 6



(A)
Planar MR for C
(C0° vs. C90°)
Planar MR for M
(M0° vs. M90°)
non-Planar MR for M
(M90° vs. C90°)
-3 μV
0 μV
3 μV
300-350ms
350-400ms
400-450ms
450-500ms
500-550ms
550-600ms
600-650ms
650-700ms
700-750ms
750-800ms
800-850ms
(B)
-2
8
600
mean amplitude (μV)
C90°
C0°
M90°
M0°
(C)
-3
3
500
time (ms)
Planar MR for C
(C0° vs. C90°)
Planar MR for M
(M0° vs. M90°)
non-Planar MR for M
(M90° vs. C90°)

Figure 7

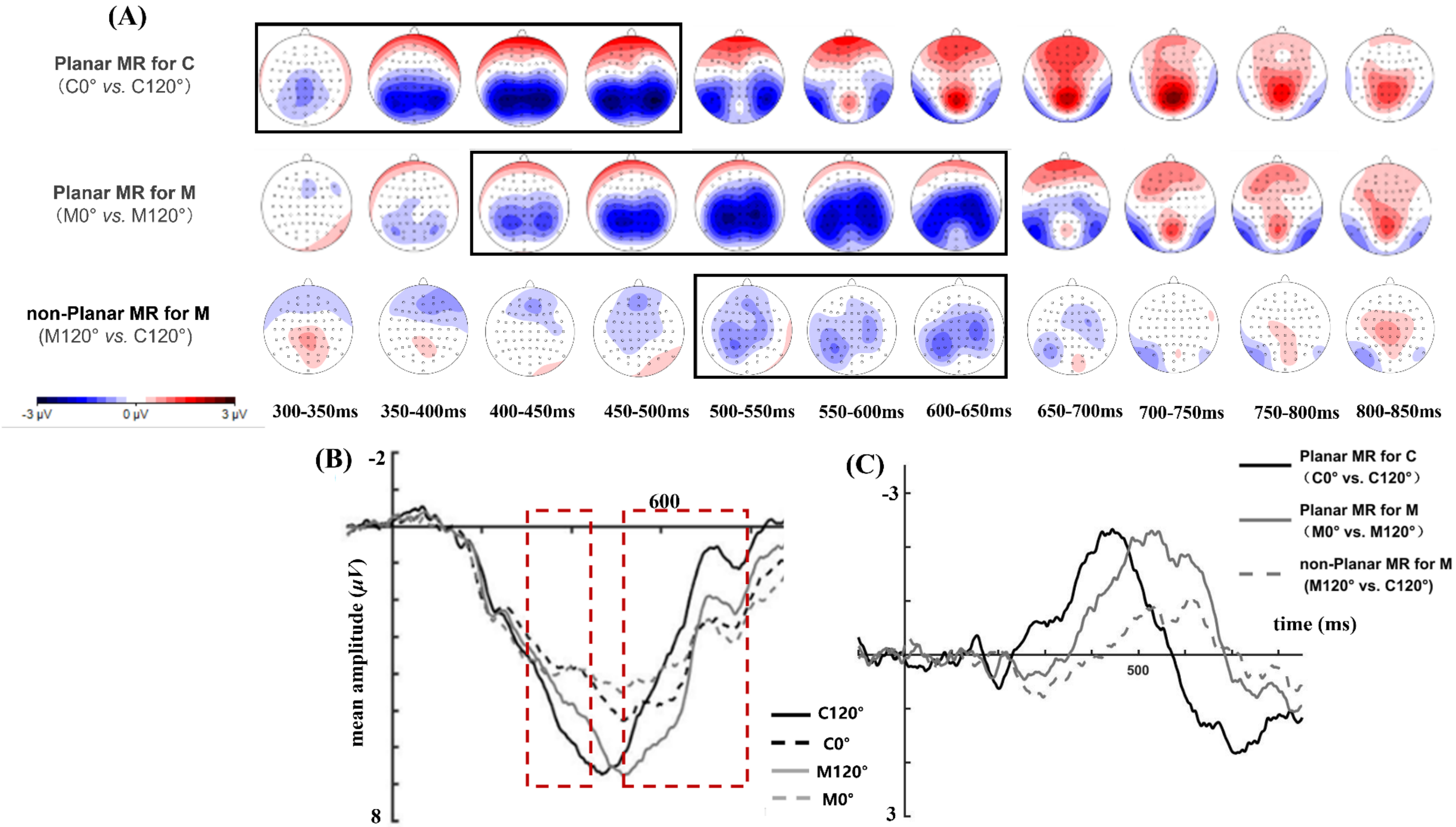
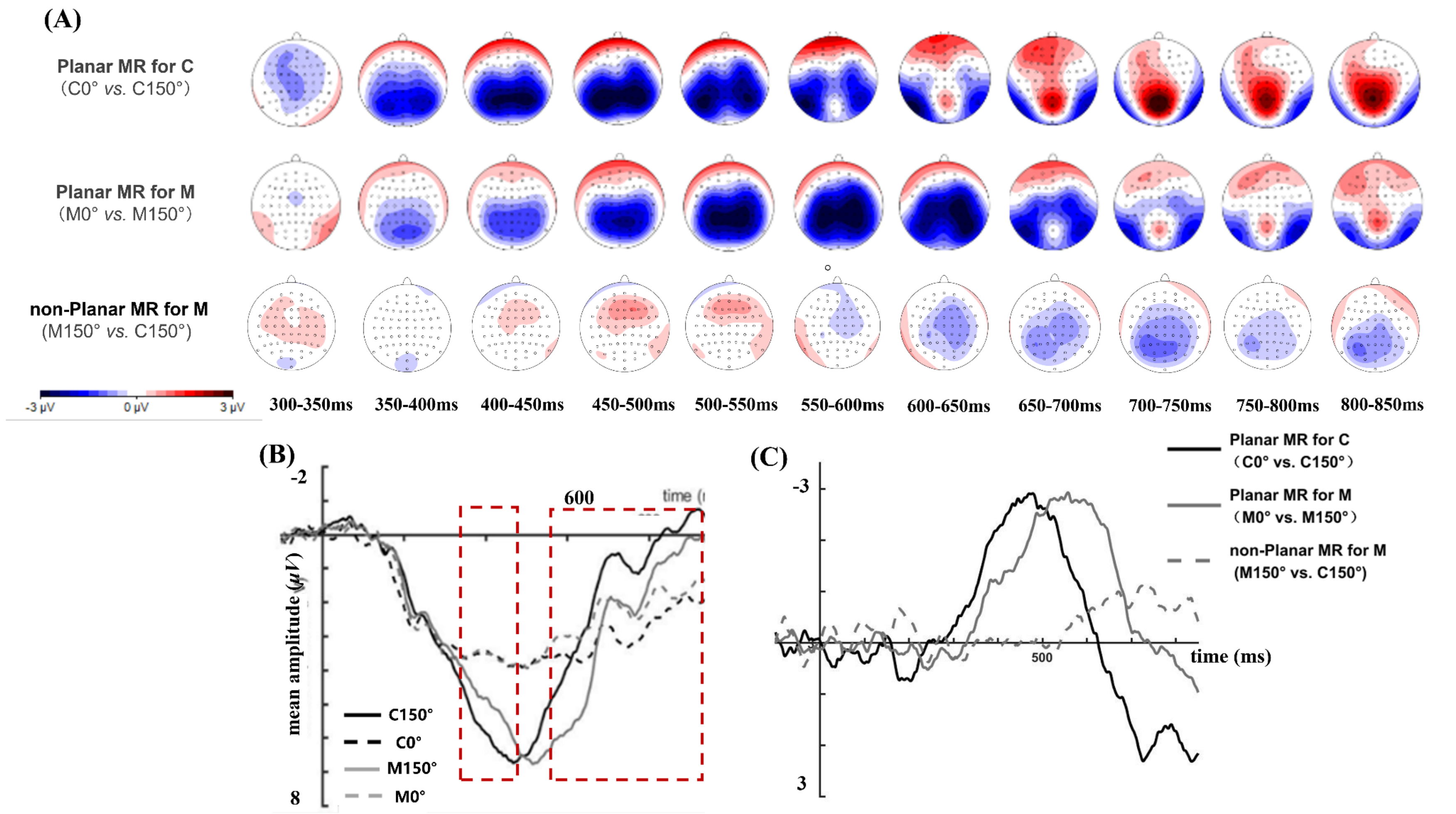

(A)
Planar MR for C
(C0° vs. C120°)
Planar MR for M
(M0° vs. M120°)
non-Planar MR for M
(M120° vs. C120°)
-3 μV
0 μV
3 μV
300-350ms
350-400ms
400-450ms
450-500ms
500-550ms
550-600ms
600-650ms
650-700ms
700-750ms
750-800ms
800-850ms
(B)
-2
600
mean amplitude (μV)
8
C120°
C0°
M120°
M0°
(C)
-3
500
3
time (ms)
Planar MR for C
(C0° vs. C120°)
Planar MR for M
(M0° vs. M120°)
non-Planar MR for M
(M120° vs. C120°)

Figure 8



(A)
Planar MR for C
(C0° vs. C150°)
Planar MR for M
(M0° vs. M150°)
non-Planar MR for M
(M150° vs. C150°)
-3 µV
0 µV
3 µV
300-350ms
350-400ms
400-450ms
450-500ms
500-550ms
550-600ms
600-650ms
650-700ms
700-750ms
750-800ms
800-850ms
(B)
-2
600
mean amplitude (µV)
C150°
C0°
M150°
M0°
8
(C)
-3
3
500
time (ms)
Planar MR for C
(C0° vs. C150°)
Planar MR for M
(M0° vs. M150°)
non-Planar MR for M
(M150° vs. C150°)

Table 1

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 30° from 300 to 850ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	**Planar rotation (C)** **C0° vs. C30°**	**Planar rotation (M)** **M0° vs. M30°**	**non-Planar rotation (30°)** **C30° vs. M30°**
300-350ms	n.s.	n.s.	$F_c(1,30) = 5.07$, $p_c = .032$, $\eta^2 = .14$
350-400ms	n.s.	n.s.	$F_c(1,30) = 18.63$, $p_c < .001$, $\eta^2 = .38$
400-450ms	n.s.	n.s.	$F_c(1,30) = 34.52$, $p_c < .001$, $\eta^2 = .54$
450-500ms	n.s.	n.s.	$F_c(1,30) = 14.54$, $p_c = .001$, $\eta^2 = .33$
500-550ms	n.s.	$F_c(1,30) = 4.61$, $p_c = .040$, $\eta^2 = .20$	n.s.
550-600ms	n.s.	$F_c(1,30) = 7.91$, $p_c = .036$, $\eta^2 = .21$	n.s.
600-650ms	$F_c(1,30) = 4.71$, $p_c = .038$, $\eta^2 = .14$	$F_c(1,30) = 5.87$, $p_c = .022$, $\eta^2 = .16$	$F_c(1,30) = 7.48$, $p_c = .01$, $\eta^2 = .20$
650-700ms	n.s.	n.s.	$F_c(1,30) = 13.82$, $p_c = .001$, $\eta^2 = .32$
700-750ms	n.s.	n.s.	$F_c(1,30) = 23.51$, $p_c < .001$, $\eta^2 = .44$
750-800ms	n.s.	n.s.	$F_c(1,30) = 14.03$, $p_c = .001$, $\eta^2 = .32$
800-850ms	n.s.	n.s.	$F_c(1,30) = 4.71$, $p_c = .037$, $\eta^2 = .14$

Note:
1. C, canonical letters; M, mirror-reversed letters.
2. cells with grey background show the significant results if rotated angle > 0° or canonical > mirror-reversed letters.

Table 2

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 60° from 300 to 850ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	Planar rotation (C) C0° vs. C60°	Planar rotation (M) M0° vs. M60°	non-Planar rotation (60°) C60° vs. M60°
300-350ms	n.s.	n.s.	n.s.
350-400ms	$F_c(1,30)=4.81$, $p_c=.036$, $\eta^2=.14$	$F_c(1,30)=4.10$, $p_c=.052$, $\eta^2=.12$	$F_c(1,30)=8.41$, $p_c=.007$, $\eta^2=.22$
400-450ms	n.s.	$F_c(1,30)=12.80$, $p_c=.001$, $\eta^2=.35$	$F_c(1,30)=33.70$, $p_c<.001$, $\eta^2=.53$
450-500ms	n.s.	$F_c(1,30)=8.08$, $p_c=.008$, $\eta^2=.29$	$F_c(1,30)=20.04$, $p_c<.001$, $\eta^2=.40$
500-550ms	n.s.	$F_c(1,30)=12.80$, $p_c=.001$, $\eta^2=.35$	$F_c(1,30)=6.67$, $p_c=.015$, $\eta^2=.18$
550-600ms	n.s.	$F_c(1,30)=8.08$, $p_c=.008$, $\eta^2=.27$	n.s.
600-650ms	$F_c(1,30)=9.72$, $p_c=.004$, $\eta^2=.24$	$F_c(1,30)=11.03$, $p_c=.002$, $\eta^2=.27$	n.s.
650-700ms	$F_c(1,30)=6.89$, $p_c=.013$, $\eta^2=.19$	n.s.	$F_c(1,30)=8.38$, $p_c=.007$, $\eta^2=.22$
700-750ms	n.s.	n.s.	$F_c(1,30)=17.43$, $p_c<.001$, $\eta^2=.37$
750-800ms	n.s.	n.s.	$F_c(1,30)=15.62$, $p_c<.001$, $\eta^2=.34$
800-850ms	n.s.	n.s.	$F_c(1,30)=10.60$, $p_c=.003$, $\eta^2=.26$

Note:
1. C, canonical letters; M, mirror-reversed letters.
2. cells with grey background show the significant results if rotated angle > 0° or canonical > mirror-reversed letters.

Table 3

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 90° from 300 to 850ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	Planar rotation (C)	Planar rotation (M) M0° vs. M90°	non-Planar rotation (90°) C90° vs. M90°
300-350ms	F_c (1,30)=4.25, p_c =.048, η^2 =.19	n.s.	n.s.
350-400ms	F_c (1,30)=15.87, p_c < .001, η^2=.39	n.s.	n.s.
400-450ms	F_c (1,30)=15.87, p_c < .001, η^2 = .39	F_c (1,30)=26.00, p_c <.001, η^2 = .46	F_c (1,30)= 9.51, p_c =.004, η^2=.24
450-500ms	F_c (1,30)= 4.61, p_c = .040, η^2 = .20	F_c (1,30)=20.27, p_c <.001, η^2 = .55	F_c (1,30)=23.90, p_c < .001, η^2 =.45
500-550ms	n.s.	F_c (1,30)=20.27, p_c <.001, η^2 = .59	F_c (1,30)=31.79, p_c <.001, η^2=.51
550-600ms	n.s.	F_c (1,30)=13.93, p_c = .001, η^2 = .37	F_c (1,30)=4.03, p_c =.054, η^2=.51
600-650ms	F_c (1,30)= 12.04, p_c =.002, η^2 = .29	F_c (1,30)=5.90, p_c = .022, η^2 = .16	n.s.
650-700ms	F_c (1,30)= 12.78, p_c =.001, η^2 = .30	n.s.	F_c (1,30)=4.11, p_c =.051, η^2=.12
700-750ms	F_c (1,30)=16.40, p_c < .001, η^2 = .35	F_c (1,30)= 4.15, p_c = .050, η^2 = .12	F_c (1,30)=4.60, p_c =.040, η^2=.13
750-800ms	F_c (1,30)= 12.92, p_c =.001, η^2 = .30	F_c (1,30)= 6.14, p_c = .020, η^2 = .17	F_c (1,30)=9.92, p_c =.004, η^2=.25
800-850ms	F_c (1,30)= 8.40, p_c = .007, η^2 = .22	F_c (1,30)= 8.70, p_c =.006, η^2 = .22	F_c (1,30)=10.80, p_c =.003, η^2=.27

Note:
1. C, canonical letters; M, mirror-reversed letters.
2. cells with grey background show the significant results if rotated angle > 0° or canonical > mirror-reversed letters.

Table 4.

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 120° from 300 to 850ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Note:

Time	Planar rotation (C)	Planar rotation (M) M0° vs. M120°	non-Planar rotation (120°) C120° vs. M120°
300-350ms	F_c (1,30)= 9.72, p_c = .004, η^2 = .32	n.s.	n.s.
350-400ms	F_c (1,30)=20.27, p_c <.001, η^2 = .54	n.s.	n.s.
400-450ms	F_c (1,30)=20.32, p_c <.001, η^2 = .62	F_c (1,30)=13.93, p_c = .001, η^2 = .37	n.s.
450-500ms	F_c (1,30)=20.29, p_c <.001, η^2 = .58	F_c (1,30)=20.27, p_c <.001, η^2 = .55	n.s.
500-550ms	n.s.	F_c (1,30)=20.27, p_c <.001, η^2 = .63	F_c (1,30)= 8.13, p_c = .008, η^2 = .21
550-600ms	n.s.	F_c (1,30)=20.27, p_c <.001, η^2 = .55	F_c (1,30)= 7.59, p_c = .01, η^2 = .20
600-650ms	F_c (1,30)= 8.64, p_c = .006, η^2 = .22	F_c (1,30)=22.47, p_c < .001, η^2 = .43	F_c (1,30)= 17.32, p_c < .001, η^2 =.37
650-700ms	F_c (1,30)=15.93, p_c < .001, η^2 = .35	n.s.	n.s.
700-750ms	F_c (1,30)=24.37, p_c < .001, η^2 = .45	F_c (1,30)= 4.80, p_c = .037, η^2 = .14	n.s.
750-800ms	F_c (1,30)=17.80, p_c < .001, η^2 = .37	F_c (1,30)= 6.83, p_c = .014, η^2 = .18	n.s.
800-850ms	F_c (1,30)=16.24, p_c <.001, η^2 = .35	F_c (1,30)= 14.40, p_c =.001, η^2 = .33	n.s.

1. C, canonical letters; M, mirror-reversed letters.
2. cells with grey background show the significant results if rotated angle > 0° or canonical > mirror-reversed letters.

Table 5

Summary of main effects of stimulus type, rotation angle, or the stimulus type × rotation angle interactions for letters rotated with 150° from 300 to 850ms post-stimulus as well as the corresponding significant post-hoc comparisons.

Time	Planar rotation (C)	Planar rotation (M) M0° vs. M150°	non-Planar rotation (150°) C150° vs. M150°
300-350ms	F_c (1,30)=4.09, p_c =.052, η^2=.19	n.s.	n.s.
350-400ms	F_c (1,30)=20.27, p_c<.001, η^2= .57	F_c (1,30)= 8.10, p_c = .008, η^2 = .28	n.s.
400-450ms	F_c (1,30)=20.27, p_c <.001, η^2=.61	F_c (1,30)=16.82, p_c <.001, η^2 = .41	n.s.
450-500ms	F_c (1,30)=20.27, p_c<.001, η^2= .63	F_c (1,30)=20.32, p_c <.001, η^2 = .59	n.s.
500-550ms	F_c (1,30)=20.25, p_c<.001, η^2=.51	F_c (1,30)=20.30, p_c <.001, η^2 = .53	n.s.
550-600ms	n.s.	F_c (1,30)=20.31, p_c <.001, η^2 = .71	n.s.
600-650ms	n.s.	F_c (1,30)=20.30, p_c <.001, η^2 = .61	F_c (1,30)=4.80, p_c= .037, η^2 = .14
650-700ms	F_c (1,30)=8.24, p_c =.008, η^2=.22	F_c (1,30)=6.12, p_c =.019, η^2 = .17	F_c (1,30)=7.64, p_c= .010, η^2 = .20
700-750ms	F_c (1,30)=24.47, p_c <.001, η^2=.45	n.s.	F_c (1,30)= 17.21, p_c < .001, η^2 =.36
750-800ms	F_c(1,30)=18.63, p_c<.001, η^2= .38	n.s.	F_c (1,30)= 5.32, p_c= .028, η^2 =.15
800-850ms	F_c(1,30)=28.61, p_c<.001, η^2= .49	F_c (1,30)=4.33, p_c =.046, η^2 = .13	F_c (1,30)= 9.50, p_c=.004, η^2 =.24

Note:
1. C, canonical letters; M, mirror-reversed letters.
2. cells with grey background show the significant results if rotated angle > 0° or canonical > mirror-reversed letters.

Figures Captions

Figure 1. Examples of canonical and mirror-reversed letters used as stimuli in the present study (A) and experimental procedure.

Figure 2. Behavioural performance in the canonical (black solid line) and mirror-reversed conditions (grey dotted line). The left panel depicts the accuracy rates and the right panel shows the response times across all the rotation angles (0°, 30°, 60°, 90°, 120° and 150°) under the two different experimental conditions.

Figure 3. Grand-averaged ERPs elicited at pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) in the 400-ms interval after letter onset. The left panel shows ERPs elicited by canonical letters while the right panel shows ERPs elicited by mirror-reversed letters as a function of the different rotation angles (0°, 30°, 60°, 90°, 120° and 150°, shown in different colors).

***Figure 4.* 30° rotation angle.** The top panel (Panel A) shows the topographic maps observed in consecutive 50ms time windows, from 300 to 850ms post-stimulus. Each row shows the scalp distribution of a different MR process. The top row shows the scalp distribution of the *Planar MR of Canonical letters (*difference between ERPs elicited by rotated canonical letters, C30°, and upright canonical letters, C0°). The middle row shows the *Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed letters, M30°, and upright mirror-reversed, M0°), while the bottom row shows the *Non-Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed, M30°, and rotated canonical letters, C30°). In Panel A, time windows in which the effects of rotation were significant are marked with a black frame. The bottom left panel (Panel B) shows ERP waveforms elicited at pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for 30° rotation angle (dotted line) and upright letters (0°, solid line), separately for canonical (black) and mirror-reversed letters (grey). Here, the time window(s) in which rotation angle x stimulus type interactions were significant is (are) marked with a red box. The bottom right panel (Panel C) shows the corresponding difference ERP waveforms reflecting the Planar MR of Canonical letters (C30° - C0°, black solid line), the *Planar MR of Mirror-Reversed letters (*M30° - M0°, grey solid line) and *non-Planar MR of Mirror-Reversed letters* (M30° - C30°, grey dotted line).

***Figure 5*. 60° rotation angle.** The top panel (Panel A) shows the topographic maps observed in consecutive 50ms time windows, from 300 to 850ms post-stimulus. Each row shows the scalp distribution of a different MR process. The top row shows the scalp distribution of the *Planar MR of Canonical letters (*difference between ERPs elicited by rotated canonical letters, C60°, and upright canonical letters, C0°). The middle row shows the *Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed letters, M60°, and upright mirror-reversed, M0°), while the bottom row shows the *Non-Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed, M60°, and rotated canonical letters, C60°). In Panel A, time windows in which the effects of rotation were significant are

marked with a black frame. The bottom left panel (Panel B) shows ERP waveforms elicited at pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for 60° rotation angle (dotted line) and upright letters (0°, solid line), separately for canonical (black) and mirror-reversed letters (grey). Here, the time window(s) in which rotation angle x stimulus type interactions were significant is (are) marked with a red box. The bottom right panel (Panel C) shows the corresponding difference ERP waveforms reflecting the Planar MR of Canonical letters (C60° - C0°, black solid line), the *Planar MR of Mirror-Reversed letters (*M60° - M0°, grey solid line) and *non-Planar MR of Mirror-Reversed letters* (M60° - C60°, grey dotted line).

Figure 6. **90° rotation angle.** The top panel (Panel A) shows the topographic maps observed in consecutive 50ms time windows, from 300 to 850ms post-stimulus. Each row shows the scalp distribution of a different MR process. The top row shows the scalp distribution of the *Planar MR of Canonical letters (*difference between ERPs elicited by rotated canonical letters, C90°, and upright canonical letters, C0°). The middle row shows the *Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed letters, M90°, and upright mirror-reversed, M0°), while the bottom row shows the *Non-Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed, M90°, and rotated canonical letters, C90°). In Panel A, time windows in which the effects of rotation were significant are marked with a black frame. The bottom left panel (Panel B) shows ERP waveforms elicited at pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for 90° rotation angle (dotted line) and upright letters (0°, solid line), separately for canonical (black) and mirror-reversed letters (grey). Here, the time window(s) in which rotation angle x stimulus type interactions were significant is (are) marked with a red box. The bottom right panel (Panel C) shows the corresponding difference ERP waveforms reflecting the Planar MR of Canonical letters (C90° - C0°, black solid line), the *Planar MR of Mirror-Reversed letters (*M90° - M0°, grey solid line) and *non-Planar MR of Mirror-Reversed letters* (M90° - C90°, grey dotted line).

Figure 7. **120° rotation angle.** The top panel (Panel A) shows the topographic maps observed in consecutive 50ms time windows, from 300 to 850ms post-stimulus. Each row shows the scalp distribution of a different MR process. The top row shows the scalp distribution of the *Planar MR of Canonical letters (*difference between ERPs elicited by rotated canonical letters, C120°, and upright canonical letters, C0°). The middle row shows the *Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed letters, M120°, and upright mirror-reversed, M0°), while the bottom row shows the *Non-Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed, M120°, and rotated canonical letters, C120°). In Panel A, time windows in which the effects of rotation were significant are marked with a black frame. The bottom left panel (Panel B) shows ERP waveforms elicited at pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for 120° rotation angle (dotted line) and upright letters (0°, solid line), separately for canonical (black) and mirror-reversed letters (grey). Here, the time window(s) in which rotation angle x stimulus type interactions were significant is (are) marked with a red box. The bottom right panel (Panel C) shows the corresponding difference ERP waveforms reflecting the Planar

MR of Canonical letters (C120° - C0°, black solid line), the *Planar MR of Mirror-Reversed letters (*M120° - M0°, grey solid line) and *non-Planar MR of Mirror-Reversed letters* (M120° - C120°, grey dotted line).

Figure 8. **150° rotation angle.** The top panel (Panel A) shows the topographic maps observed in consecutive 50ms time windows, from 300 to 850ms post-stimulus. Each row shows the scalp distribution of a different MR process. The top row shows the scalp distribution of the *Planar MR of Canonical letters (*difference between ERPs elicited by rotated canonical letters, C150°, and upright canonical letters, C0°). The middle row shows the *Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed letters, M150°, and upright mirror-reversed, M0°), while the bottom row shows the *Non-Planar MR of Mirror-Reversed letters (*difference between rotated mirror-reversed, M150°, and rotated canonical letters, C150°). In Panel A, time windows in which the effects of rotation were significant are marked with a black frame. The bottom left panel (Panel B) shows ERP waveforms elicited at pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) for 150° rotation angle (dotted line) and upright letters (0°, solid line), separately for canonical (black) and mirror-reversed letters (grey). Here, the time window(s) in which rotation angle x stimulus type interactions were significant is (are) marked with a red box. The bottom right panel (Panel C) shows the corresponding difference ERP waveforms reflecting the Planar MR of Canonical letters (C150° - C0°, black solid line), the *Planar MR of Mirror-Reversed letters (*M150° - M0°, grey solid line) and *non-Planar MR of Mirror-Reversed letters* (M150° - C150°, grey dotted line).

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