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One turn at a time: Behavioral and ERP evidence for two types of rotations in the classical mental rotation task

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Abstract

We perform mental rotations in many everyday situations, such as reading a map or following furniture assembling instructions. In a classical mental rotation task, participants are asked to judge whether a rotated stimulus is presented in its mirrored form or its canonical form. Previous results have indicated a degree effect: RT is longer as the angle of rotation increases, and this effect is traditionally explained by arguing that this judgment requires rotating the stimulus back to its upright form. Importantly, in half of the trials, the stimuli are rotated on both the page plane and mirror plane. Namely, we argue that in previous research the task actually involved two different rotation processes. To provide a clear dissociation between these two rotations, we collected EEG data and used the Contralateral Delay Activity (CDA) as an indicator of visual working memory (VWM) load. The results of Experiment 1 suggested different VWM involvement according to the degrees rotations when the item was not mirrored, such that the CDA amplitude generally increased as the degree of rotation was higher. Mirrored trials were all at ceiling in terms of CDA, regardless of their rotation degree. Experiment 2 showed increased CDA amplitude uniquely related to the flip rotation. Thus, we provided ERP evidence that the canonical mental rotation task involves two types of rotations that can be dissociated based on the load they imposed on VWM.

KEYWORDS

contralateral delayed activity, ERPs, mental rotation, visual working memory

1 | INTRODUCTION

Mental rotation is the process in which we rotate visual representations in our minds. For example, when we read a map, we sometimes need to rotate the map in our mind such that it applies to the road ahead. Mental rotation processes are involved in situations such as navigating, playing Tetris or following furniture assembling instructions. Evaluating an individual's mental rotation ability is part of the Woodcock–Johnson IQ test, further supporting its importance even as an aptitude measure (e.g., Woodcock et al., 2003).

One of the classic mental rotation paradigms involves letters presented in their upright form or in their mirrored form and rotated at different degrees. In this mirror image task, participants are asked to recognize whether the rotated letter is presented in its canonical upright or mirrored form (e.g., Alivisatos & Petrides, 1996; Cooper & Shepard, 1973; Prime & Jolicoeur, 2010). The underlying assumption is that the participants mentally rotate the letter in their minds until they can perform the required judgment. A similar assumption is relevant for another common mental rotation task in which two stimuli are presented side by side, each at a different angle, and participants are required to decide whether the two stimuli are identical or not. The assumption is that one of the items is being rotated until reaching a similar angle, and at this point comparing the items becomes possible (Shepard & Metzler, 1971). It has also been suggested that mental rotation that takes place before stimulus presentation is similar in rate to mental rotation after stimulus presentation (Cooper, 1975).

Supporting these assumptions, both tasks show a degree of rotation effect, which is the main effect discussed regarding mental rotation. Namely, previous research has shown that increasing the rotation angle is followed by longer RTs (e.g., Shepard & Metzler, 1971). Presumably, the longer response times are a consequence of having to mentally rotate the target item for a longer interval as the angle increases. This is true for a familiar upright orientation of an object (e.g., Alivisatos & Petrides, 1996; Cooper & Shepard, 1973; Prime & Jolicoeur, 2010) as well as for a learned stored representation (Tarr & Pinker, 1989). In addition, it has been proposed that mental rotation might be performed in discrete steps and not continuously (Cooper & Shepard, 1973). It has also been shown that during mental rotation the process passes through intermediate stages by examining the reaction times to expected stimuli and unexpected stimuli, which were hypothesized to be intermediate steps in the process (Cooper, 1976).

While performing mental rotation, the visual representation of the object needs to be maintained and updated by visual working memory (VWM). It was argued that during mental rotation VWM is the substrate in which the representation of the stimulus is stored while it is being processed (Hyun & Luck, 2007; Prime & Jolicoeur, 2010). Moreover, previous research argued that as the rotation degree increases, the longer the item is maintained in VWM (Prime & Jolicoeur, 2010). Note that in most mental rotation tasks, the stimulus is usually present on the screen until participants make the required judgment. Importantly, it has been shown that VWM is used even when the items are still within view (Balaban & Luria, 2020; Luria & Vogel, 2014; Tsubomi et al., 2013).

Prime and Jolicoeur (2010) investigated the role of VWM during mental rotation using the contralateral delay activity ERP component (CDA; referred to by them as the SPCN component), which is a marker of VWM capacity. Previous studies identified parietal cortex regions as the origin of the CDA, which is in line with fMRI findings (Luria et al., 2016). To calculate the CDA, the amplitude of the ipsilateral side relative to the target on the screen is subtracted from the contralateral amplitude. The amplitude on the ipsilateral side is presumed to represent mostly low-level and early perceptual processing, whereas the amplitude on the contralateral side represents VWM-related activity as well as low-level processing. Thus, the subtraction reduces low-level processes and local noise (similar to calculating the N2pc or the LRP; cf., Luria et al., 2016; Vogel & Machizawa, 2004). The relevant side is indicated by an arrow appearing prior to the memory array.

The CDA amplitude increases as the number of items maintained in memory increase, until it reaches the individual's capacity limit (Vogel & Machizawa, 2004). The CDA was found to be highly correlated with the behavioral performance of the number of items maintained in VWM, and it has also been demonstrated that the CDA represents a marker of VWM in online processing (Balaban & Luria, 2020; Luria et al., 2016). Many articles have successfully used the CDA to infer interesting attributes regarding VWM (e.g., Balaban et al., 2018; Luria et al., 2010; Luria & Vogel, 2011; Vogel & Machizawa, 2004), and in this article, we infer a connection between a higher CDA amplitude and an increased VWM activity during mental rotation.

Prime and Jolicoeur (2010) used the mirror image task previously described, with both letters and numbers rotated at various degrees and presented either in their canonical form or their mirrored form. They found the expected mental rotation effect for the RTs, which showed higher RTs for higher rotation angles. The CDA amplitude in their experiment was not modulated by the different degrees' rotations. However, they did find a difference in the CDA offset latency, which was longer as the degree of rotation increased. Based on this result, Prime and Jolicoeur (2010) argued that the offset CDA latency reflected the duration the stimulus was maintained in VWM, such that longer offset latencies indicated the item was represented longer in VWM. In their control experiment, they used a letter–digit character classification task to show that the same rotated stimulus presented in a task that did not require mental rotation, yielded different results both in RTs and the CDA. Namely, there was no degree effect in the RTs results for the control experiment and they did not find the latency offset effect. This result supports that the mental rotation process is responsible for the offset latency effect, and not just categorizing rotated stimulus that did not require performing mental rotation.

In the current study, we would like to examine whether a mirror image task such as the one used in Prime and Jolicoeur's (2010) study, actually involves two types of rotation: rotation in the page plane, which refers to degree-rotation, and flip rotation, which is rotating a stimulus from its mirrored form. Although the mirror image task includes both types of rotation, most of the previous research analyzed and discussed only the degree effect without separating trials with canonical letters and trials with mirrored letters. Indeed, in two studies that separated the two types of rotations, a difference between the trials with mirrored letters and the canonical letters trials was found, showing faster RTs for canonical letters trials (Hamm et al., 2004; Núñez-Peña & Aznar-Casanova, 2009). Nevertheless, the degree effect was still evident in the mirrored trial RTs. To account for these results, it has been suggested that the rotations are performed sequentially: after the rotation on the page plane, another rotation is performed, from the mirrored form to the canonical form (Hamm et al., 2004; Núñez-Peña & Aznar-Casanova, 2009).

The results presented in studies using the mirror judgment task might, therefore, be misleading. Although presented as reflecting rotation on the page plane, the results might actually represent the effect of the flip rotation, or the interaction between the two types of rotations. We would like to investigate whether the flip rotation is fundamentally different from the rotation on the page plane. We examined whether there are, indeed, two types of rotations, in terms of their difficulty, as indicated by the load they impose on VWM.

Following Prime and Jolicoeur (2010), we expected to find differences in the CDA offset latency. As they explained, the differences in the offset latency are connected to the duration the items were maintained in VWM, which is connected to the degree of rotation required. To account for the differences in RTs and their possible influence on the CDA amplitude in the stimulus-locked analysis, we also analyzed the response-locked CDA data, which allowed us to control for the RTs differences (Williams & Drew, 2020). Locking the data to the response aligns the data in a way that allows us to examine the VWM load just before the response, which addressed the possibility that the stimulus-locked differences we found in amplitude might reflect differences in RTs. Namely, faster RTs could lead to freeing VWM earlier and in turn to a lower stimulus-locked CDA amplitude. If, indeed, the differences in CDA amplitude in the stimulus-locked analysis are derived from the variation of RTs between the conditions, these differences should disappear in the response-locked analysis. Instead, if the stimulus-locked amplitude differences reflect storage and processing differences, the response-locked CDA pattern should mirror the stimulus-locked pattern, and maintain the amplitude differences observed in the stimulus-locked analysis. We have added topographic maps of both the stimulus-locked and the response-locked data in Appendix A. Overall, this analysis showed similarities between the two topographic maps across conditions.

In addition to the CDA component, we have also examined the N2pc component, which is considered to reflect attentional processes (Eimer, 1996; Luck & Hillyard, 1994). The N2pc has been shown to reflect filtering processes (Luck & Hillyard, 1994), attentional selection (Eimer, 1996) and attentional engagement (e.g., Zivony et al., 2018). Previously, a larger N2pc component was shown when the task was more complex (Luck et al., 1997). This component is calculated similarly to the CDA, by subtracting the ipsilateral side from the contralateral side.

In this study, participants performed the mirror image task, but the two rotation types were analyzed separately (Experiment 1). In Experiment 2, the flip rotation was isolated, to investigate the role of VWM in this process alone, without the interaction with the degree effect. From the results of both experiments, we observed a difference in VWM load connected to the type of manipulation and to the degree of rotation.

2 | EXPERIMENT 1: PLANE-ROTATION AND FLIP-ROTATION

2.1 | Method

2.1.1 | Participants

The experiment included 18 participants (14 females) ages 18–32 (mean age 24), who received either course credit or a payment of 40 NIS (approximately 12$) per hour. The experiment was approximately 135 minutes overall. All participants had normal or corrected to normal vision, and normal color vision. In addition, all participants were native Hebrew speakers.

An a priori power analysis was conducted using G*Power3.1.9.2 (Faul et al., 2007) to test the difference between the different degrees conditions using a repeated-measures ANOVA. We used a small effect size (f = 0.32; based on the η_p^2 =0.095 effect reported by Prime & Jolicoeur, 2010), with .5 correlation among repeated measures and an alpha of .05. Results showed that a total sample of 15 was required to achieve a power of 0.80.

Participants with over 30% rejection rate in either the stimulus-locked or the response-locked analyses were replaced (three participants). One participant had less than 50% accuracy in one of the conditions and was also replaced.

2.1.2 | Stimuli and procedure

The participants filled out a consent form following the procedures of a protocol approved by the Ethics Committee at the Tel-Aviv University.

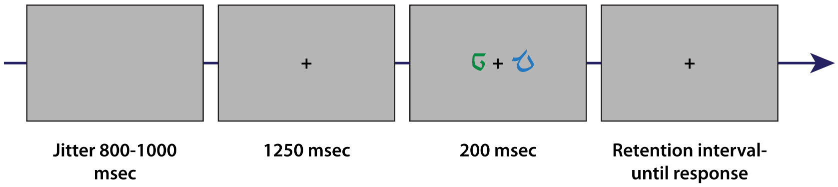

FIGURE 1 An example of a trial sequence in experiment 1. Each trial started with a blank screen, followed by a fixation, which was presented for 1250 ms. Then, the stimuli appeared on both sides of the screen for 200 ms. After their disappearance, a fixation appeared in the middle of the screen, until the participant responded.

Mental rotation task[1]

The discrimination task is illustrated in Figure 1. The stimuli were blue or green asymmetrical Hebrew characters (“ב” “ת” “פ” “ע” “מ” “ל” “ג”) rotated at different degrees (0, ±60, ±120, 180) and presented in their canonical form or mirrored form. Each letter subtended approximately 1.2°×1.2° of visual angle and was presented at a 1.9°–2.9° distance from a fixation (the location was randomly jittered). The stimuli were presented from a viewing distance of approximately 60 cm.

At the beginning of each trial, a blank screen appeared for 800 to 1000 ms (with 50 ms increments, the overall presentation duration was determined randomly), followed by a fixation (“+”) presented for 1250 ms. Then, two stimuli appeared on both sides of the screen for 200 ms, followed by a fixation, which was presented until a response was received. Each participant was assigned a target color that was the same throughout the whole experiment. The target colors were counterbalanced between participants. Participants were asked to recognize whether the letter presented in the target color was in its canonical form or in its mirrored form. The side in which the target color appeared, as well as the letter and the rotation degree, were randomized in each trial. Participants made a speeded response via button press using the “F” and “J” keys on a computer keyboard, indicating “canonical” and “mirrored,” and the buttons were counterbalanced between participants. Participants were instructed to blink immediately after they responded.

The experiment started with 60 practice trials followed by 12 blocks, with 84 trials in each block. There were approximately 126 trials per condition.

[1]Participants also performed a change detection task and questions from aptitude tests. We use these tasks to collect data about the population, as previously been done in our lab (Balaban et al., 2019). We also looked at correlations between individual VWM capacity and mental rotation performance. Since we did not find any consistent correlations across experiments, we do not report them here.

2.1.3 | Electrophysiological recording and processing

The EEG data were recorded inside a shielded Faraday cage, with a Biosemi ActiveTwo system (Biosemi B.V.), from 32 scalp electrodes at a subset of locations from the extended 10–20 system (Fp1, Fp2, AF3, AF4, F3, F4, F7, F8, Fz, FCz, C3, C4, Cz, T7, T8, P1, P2, P3, P4, P5, P6, P7, P8, Pz, PO3, PO4, PO7, PO8, POz, O1, O2, and Oz), as well as from two electrodes placed on the mastoids. EOG was recorded by two electrodes placed 1 cm laterally to the external canthi, and from an electrode beneath the left eye. Data were digitized at 256 Hz.

Offline signal processing was performed using custom Matlab (The MathWorks) scripts, the EEGLAB Toolbox (Delorme & Makeig, 2004) and the ERPLAB Toolbox (Lopez-Calderon & Luck, 2014). All the data were referenced to the average of the mastoids. The epoched data were low-pass filtered using the “eegfilt” function from the EEGLAB Toolbox (Delorme & Makeig, 2004), with a cutoff point at 30 Hz. We used a two-way least-squares FIR filtering, with a filtering order of 24. There was a high-pass filter of 0.16 Hz applied during the recording through the Biosemi software. Only trials with a correct response were included in the analysis. Both stimulus-locked and response-locked data were baseline corrected using the mean voltage during the 200 ms window immediately before stimulus onset.

CDA

A sliding window peak-to-peak analysis was used for artifact detection, with a threshold of 80 μV for the EOG electrodes, and 100 μV for the analyzed electrodes (P7, P8, PO3, PO4, PO7, and PO8), with a window size of 200 ms moving every 100 ms. Epoched data were averaged separately for each condition. The CDA and difference waves were calculated by subtracting the average activity at electrodes ipsilateral to the target side from the average activity at electrodes contralateral to the target side.

Stimulus-locked. The continuous data were epoched from −200 ms before stimulus onset to 800 ms. Artifact detection was performed on a −200 ms until 800 ms window relative to stimulus onset. This procedure resulted in a mean rejection rate of 6.25%. Statistical analysis was performed on a 400–800 ms window. The starting point of this window was based on previous research (Luria & Vogel, 2011; Pagano et al., 2014), and the end-point of the window was chosen to be 800 ms, which is earlier than the average response time in Experiment 1, which was 877 ms. Additional analysis of the CDA electrodes analyzed separately appears in Appendix B.

Response-locked. The continuous data were epoched from −700 to 200 ms relative to the response. Artifact detection was performed from −700 ms until the response (0 ms). We removed trials with RTs shorter than 400 ms (0.15% of the trials). This procedure resulted in a mean rejection rate of 8.96%. Statistical analysis was performed on a −400 to 0 ms window relative to the response following Williams and Drew (2020). In addition, to avoid trials with artifacts near the baseline, we removed all the trials that had artifacts in them in the stimulus-locked window from the response-locked analysis as well.

CDA offset latency. Offset latencies were analyzed with the threshold technique (e.g., Prime & Jolicoeur, 2010). For each condition, the threshold was set to 50% of the peak amplitude. The continuous data were epoched from −200 to 1000 ms relative to stimulus onset. This procedure resulted in a mean rejection rate of 24.70%. There were six participants with a rejection rate higher than 25%, which were included in this analysis. We analyzed here the average of PO7 and PO8 electrodes alone, to match the analysis in Prime and Jolicoeur (2010). When looking for the 50% of the peak in this time window, there was one participant with missing data for some of the conditions, who was removed from the analysis. The analysis was performed on a total of 17 participants. We analyzed only the 0, 120, and 180 degrees conditions, without separating the rotation types, and we used the jackknife approach, similar to Prime and Jolicoeur (2010).

N2pc

The analysis was similar to the CDA stimulus-locked analysis. Statistical analysis was performed on a 220–280 ms window relative to stimulus onset. Epoched data were averaged separately for each condition, and the N2pc difference waves were calculated by subtracting the average activity at electrodes ipsilateral to the target side from the average activity at electrodes contralateral to the target side.

The RRN component (Heil, 2002; Provost et al., 2013) was also analyzed, see Appendix C.

2.2 | Results

This experiment aimed to examine the differences in VWM involvement in two types of rotation—rotation on the page plane and flip rotation.

The data were aggregated and organized before the statistical analyses using prepdat (Allon & Luria, 2016). A repeated-measures ANOVA was used, with both Degrees (0, 60, 120, 180) and Letter (canonical or mirrored) as independent variables. We used a false discovery rate (FDR) procedure (Benjamini & Hochberg, 1995) to compensate for multiple comparisons. All analyzed data are available at the Open Science Framework: https://osf.io/ueb6n/.

2.2.1 | Behavioral results

The average accuracy rate was 97.7%. Detailed accuracy for each condition can be found in Appendix D.

RTs in exp. 1

RTs results are presented in Figure 2 (compared to FDR corrected alpha of .05).

The results showed the expected degree effect ($F(3, 51) = 134.45$, $p < .001$, $\eta_p^2 = 0.89$), in which the RTs were longer when the degree of rotation increased. Comparing the Letter in the different degrees showed that the 180 degrees condition yielded longer RTs than the 120 degrees condition ($F(1, 17) = 62.40$, $p < .001$, $\eta_p^2 = 0.79$). The 120 degrees condition had longer RTs than the 60 degrees condition ($F(1, 17) = 219.57$, $p < .001$, $\eta_p^2 = 0.93$). Finally, the 60 degrees condition had longer RTs than the 0 degrees condition ($F(1, 17) = 71.64$, $p < .001$, $\eta_p^2 = 0.81$).

The Mirrored trials yielded longer RTs than the Canonical trials ($F(1, 17) = 70.30$, $p < .001$, $\eta_p^2 = 0.81$), similar to previous findings (Hamm et al., 2004; Núñez-Peña & Aznar-Casanova, 2009). The interaction between Degrees and Letter was not significant ($F(3, 51) = 2.03$, $p = .12$, $\eta_p^2 = 0.11$).

2.2.2 | Stimulus-Locked CDA amplitude in exp. 1

A main effect for Degrees was found ($F(3, 51) = 22.41$, $p < .001$, $\eta_p^2 = 0.57$), generally showing an increase in CDA amplitude with a higher degree of rotation. In addition, there was a main effect for Letter ($F(1, 17) = 16.62$, $p < .001$, $\eta_p^2 = 0.49$), suggesting that the Mirrored trials taxed VWM more than the Canonical trials. There was an interaction between Degrees and Letter ($F(3, 51) = 6.74$, $p < .001$, $\eta_p^2 = 0.28$).

In the Canonical trials (see Figure 3a), there was no difference between 180 degrees and 120 degrees ($F < 1$), but analyzed together, the 180 degrees and 120 degrees conditions yielded a higher amplitude than the 60 degrees condition ($F(1, 17) = 21.07$, $p < .001$, $\eta_p^2 = 0.55$). The 60 degrees condition also had a higher CDA amplitude than the 0 degrees condition ($F(1, 17) = 14.80$, $p = .001$, $\eta_p^2 = 0.47$). The degrees effect we observed suggested more VWM involvement as the degree of rotation increased. Contrary to Prime and Jolicoeur (2010), our results showed a higher CDA amplitude as the degree of rotation increased, with the exception of the 180 degrees condition, which might indicate reaching VWM capacity limit already at 120 degrees (Vogel & Machizawa, 2004).

In the Mirrored trials (see Figure 3b), there was no difference between 180 degrees and 120 degrees ($F(1, 17) = 1.23$, $p = .28$, $\eta_p^2 = 0.07$), as well as between 180 degrees and 120 degrees compared to 60 degrees ($F < 1$). There was only a difference between 180, 120, and 60 that when averaged together had a higher amplitude compared to 0 ($F(1, 17) = 7.60$, $p = .013$, $\eta_p^2 = 0.31$). FDR yielded a corrected alpha of 0.025. These results support our argument about two types of rotations. Here we did

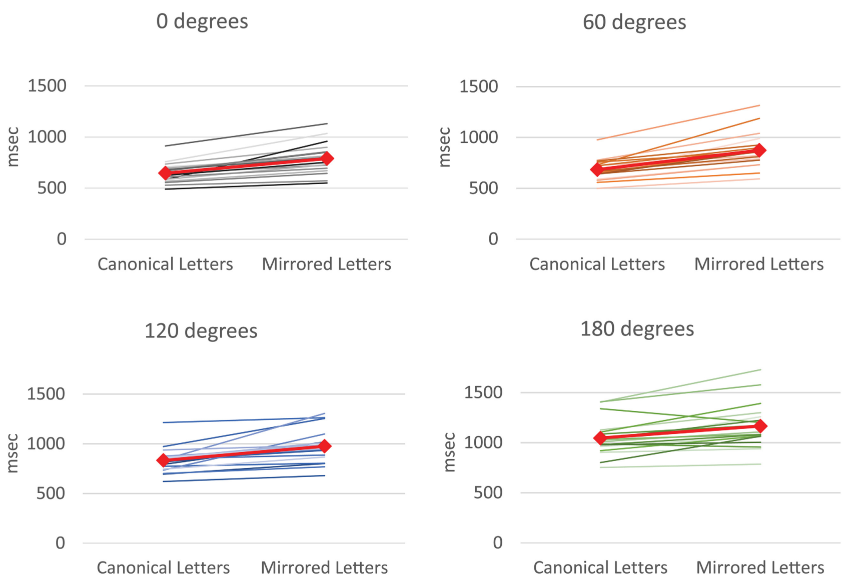

FIGURE 2 RTs in ms for experiment 1.

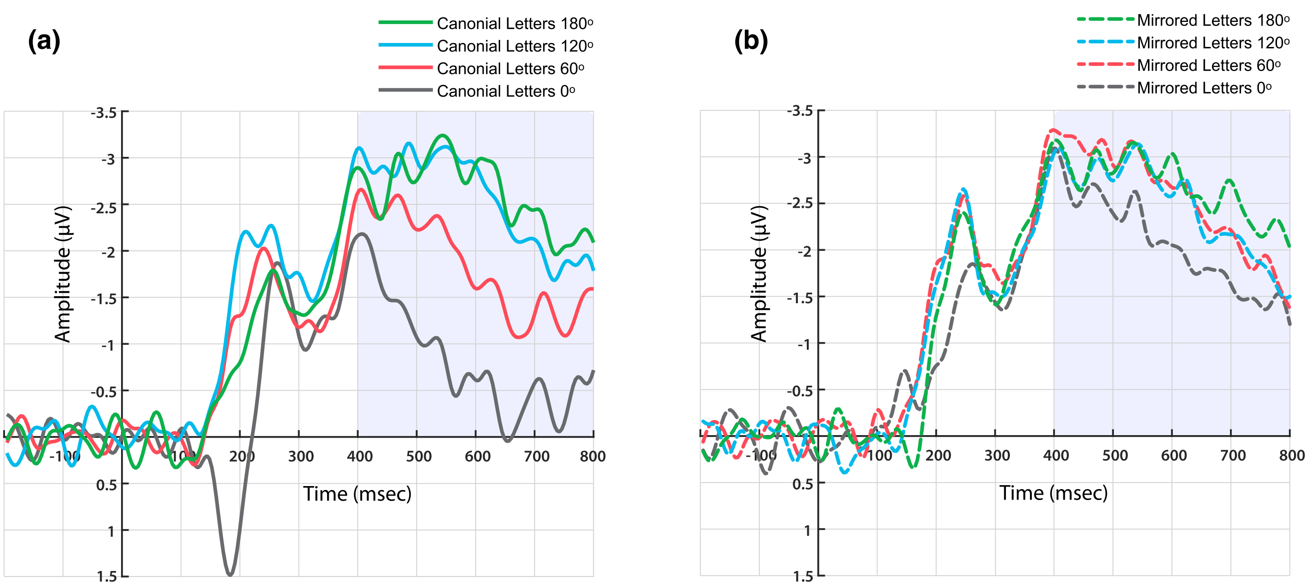

FIGURE 3 CDA amplitude for experiment 1, stimulus-locked. The amplitude is an average of the electrodes P7, P8, PO3, PO4, PO7, and PO8. Part a shows the different degrees conditions in the canonical trials and part b presents the degrees conditions in the mirrored trials. The colored rectangle marks the time window analyzed for the CDA: 400–800 ms relative to stimulus onset. The same electrodes were analyzed for the N2pc as well, in a 220–280 ms window.

not observe a degree effect, but only a difference between having to perform two rotations in the 60, 120, and 180 conditions (rotation on the page plane and flip rotation) and having to perform only one rotation in the 0 degrees condition (only flip rotation). This could be explained by the CDA reaching its asymptote when performing two rotations.

It is noteworthy that Prime and Jolicoeur (2010) reported somewhat different results. Namely, in their study the degrees effect was evident only in the CDA offset latency. We argue that there are several differences between their design and the current one, as well as in the analysis, which may account for the different patterns of results. First, Prime and Jolicoeur analyzed the two rotation types (rotation on the page plane and flip rotation) together. In addition, they did not use a 60 degrees condition, but only 0, 120, and 180 degrees. Moreover, for the CDA analysis, they used a time window of 50 ms. This is a relatively short time window (e.g., Vogel & Machizawa, 2004). In the current analysis, we used a 400 ms window. Another important difference is that Prime and Jolicoeur (2010) used a low-pass filter of 8 Hz, which can cause distortions of the data (Luck, 2014). We used a 30 Hz cutoff as was used in our lab by default (e.g., Allon et al., 2014; Drew et al., 2018). Finally, they analyzed only the PO7 and PO8 electrodes, whereas we analyzed the average of P7, P8, PO3, PO4, PO7, and PO8. When we analyzed our results in the same manner, meaning analyzing both rotations together, without the 60 degrees condition, using the same 50 ms time window for PO7 and PO8 only, the statistical power of the effect was, indeed, lower ($F(2, 34) = 2.18$, $p = .129$, $\eta_p^2 = 0.11$).

The results so far supported the hypothesis that there is another process happening in addition to the rotation on the page plane. We observed higher RTs in trials that included mirrored letters. In addition, the CDA showed a different pattern between the Mirrored trials and the Canonical trials: While the CDA amplitude in the Canonical trials showed a degrees effect (i.e., an increase in amplitude as the rotation degrees increased up to 120 degrees), the Mirrored trials showed only a difference between performing one or two rotations (0 degrees vs. 60, 120, or 180 degrees).

Next, we wanted to verify that the differences found in the CDA amplitude between the various degrees conditions do not simply reflect the difference in RTs between these conditions. To that end, we analyzed the CDA locked to the response, so that the different RTs between the conditions will not influence the time point of comparison. Thus, any differences in the CDA amplitude could not be accounted for by differences in RTs (Williams & Drew, 2020).

2.2.3 | Response-Locked CDA amplitude in exp. 1

The results for the response-locked analysis mostly replicated the results observed in the stimulus-locked analysis. The overall pattern indicated that in both the stimulus-locked and response-locked analyses, the degrees differences are apparent mostly in the canonical letters condition and not in the mirrored letters condition that showed asymptote amplitude for most degrees conditions.

A main effect for Degrees was found ($F(3, 51) = 4.77$, $p = .005$, $\eta_p^2 = 0.22$), generally showing an increase in CDA amplitude with a higher degree of rotation. There was no main effect for Letter ($F(1, 17) = 1.85$, $p = .192$, $\eta_p^2 = 0.10$). There was an interaction between Degrees and Letter ($F(3, 51) = 4.35$, $p = .008$, $\eta_p^2 = 0.20$).

In the Canonical trials (see Figure 4a), there was a trend showing a higher amplitude in the 120 degrees relative to the 180 degrees, but this trend was not significant ($F(1, 17) = 4.17$, $p = .057$, $\eta_p^2 = 0.20$). The 120 degrees condition yielded a higher amplitude than the 60 degrees condition similar to the stimulus-locked analysis ($F(1, 17) = 5.81$, $p = .027$, $\eta_p^2 = 0.25$), though this difference just missed significance after FDR correction, compared to a corrected alpha of 0.025. The 60 degrees condition had a significantly higher CDA amplitude than the 0 degrees condition similar to the stimulus-locked analysis ($F(1, 17) = 6.56$, $p = .02$, $\eta_p^2 = 0.28$).

In the Mirrored trials (see Figure 4b), there was no difference between 180 degrees and 120 degrees ($F < 1$), similar to the stimulus-locked analysis. There was a trend showing that 180 degrees and 120 degrees averaged together had a higher CDA amplitude relative to 60 degrees ($F(1, 17) = 4.72$, $p = .044$, $\eta_p^2 = 0.22$), though this effect was not significant after FDR correction. There was no difference between the 60 degrees compared to 0 degrees ($F < 1$).

2.2.4 | CDA offset analysis for the stimulus-locked data in exp. 1

To replicate Prime and Jolicoeur (2010), we analyzed the CDA offset interval using similar parameters as the original analysis. We found a main effect for the degrees in the offset latencies ($F[2,32] = 10.13$, $p < .001$), similar to Prime and Jolicoeur (2010). When looking at the pairwise comparisons, the latency for 120 degrees (630 ms) was longer than 0 degrees (530 ms; $F[1,16] = 17.39$, $p < .001$), as well as 180 degrees (671 ms) compared to 0 degrees ($F[1,16] = 20.18$, $p < .001$). However, we did not find a significant difference between 120 degrees and 180 degrees

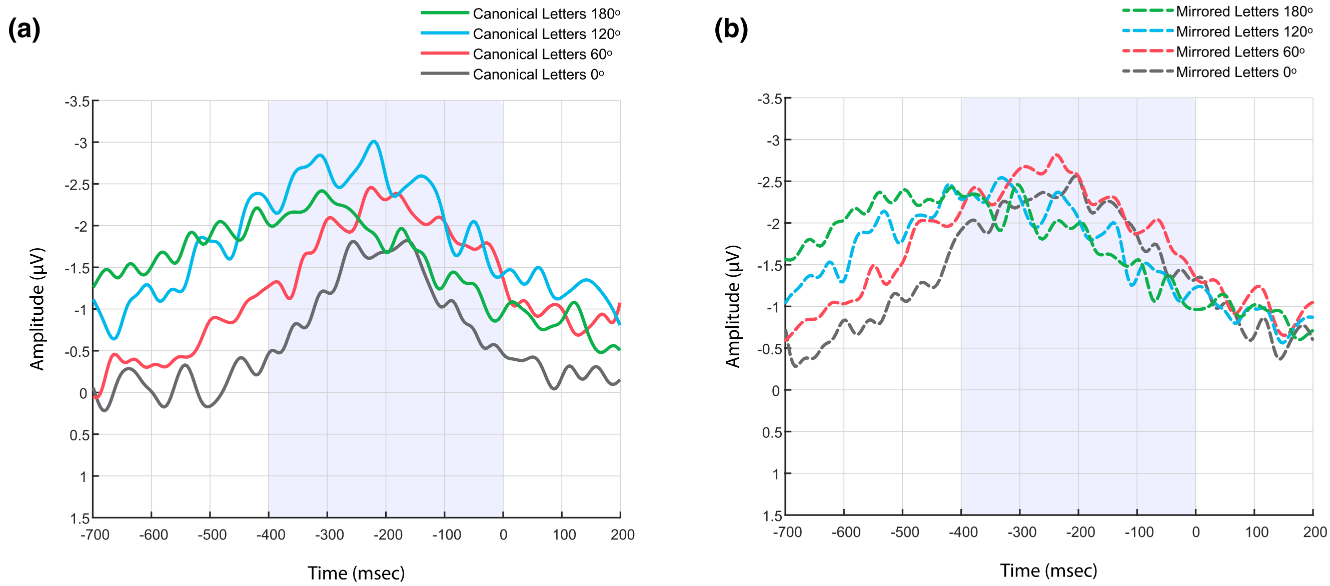

FIGURE 4 CDA amplitude for experiment 1, response-locked. The amplitude is an average of the electrodes P7, P8, PO3, PO4, PO7, and PO8. Part a shows the different degrees conditions in the canonical trials and part b presents the degrees conditions in the mirrored trials. The colored rectangle marks the time window analyzed for the CDA: −400 to 0 ms relative to the response.

(F[1,16] = 1.11, p =.307). Numerically this pattern of results replicates the findings by Prime and Jolicoeur (2010), though the last difference was not significant.

2.2.5 | Post –hoc analysis: N2pc

We had no specific a-priori hypothesis regarding the N2pc component, but since we observed a large modulation of the N2pc component, we decided to analyze and report these effects. Our N2pc results showed a different pattern relative to the CDA amplitude analysis.

Just before the observed N2pc spike, we observed an early positive spike for the Canonical letters in the 0 degrees condition. Without using any formal statistics, we observed that this spike was present in 75% of our participants, and though we are not sure what this spike represents, it does not seem to be an outlier. We chose a time window of 220 ms until 280 ms to not include this spike in the N2pc analysis.

N2pc results (see Figure 3) showed a main effect for Degrees ($F(3, 51) = 5.71$, $p = .002$, $\eta_p^2 = 0.25$), as well as a main effect for Letter ($F(1, 17) = 11.44$, $p = .004$, $\eta_p^2 = 0.40$). In the Letter main effect, the Mirrored condition yielded a higher N2pc amplitude than the Canonical condition. This indicates an early difference between the two types of rotations. Looking at the degrees effect, the difference between the 180 degrees condition and the 120 degrees condition was not significant ($F(1, 17) = 1.85$, $p = .19$, $\eta^2 = 0.10$) as well as between the180 and the 120 degrees conditions compared to the 60 degrees condition ($F(1, 17) = 1.36$, $p = .26$, $\eta^2 = 0.07$). The amplitude of the 180, 120 and 60 degrees conditions averaged together was higher than the 0 degrees condition ($F(1, 17) = 9.65$, $p = .006$, $\eta^2 = 0.36$). This suggests a higher N2pc amplitude when the letter had an angle relative to the zero rotation condition. The interaction between Degrees and Letter was not significant ($F < 1$).

Experiment 1 only showed a difference between the flip and plane rotation under the context of plane rotation. The goal of Experiment 2 was to verify whether we can find different VWM involvement in the mirror rotation even when there is no need for a plane rotation.

3 | EXPERIMENT 2: FLIP-ROTATION ALONE

The results of Experiment 1 showed evidence for two types of rotations based on VWM involvement. Experiment 1 showed a difference between the two rotation processes. The Flip rotation required an additional VWM involvement than just rotation on the page plane. Moreover, the addition of flip rotation eliminated the degree's effect in the CDA amplitude.

Although the degree effect has been researched extensively, the flip rotation has received much less attention and was investigated only in addition to the degree rotation process. The goal of this experiment was to isolate the flip rotation and examine it without the context of the degrees conditions. Accordingly, this experiment included

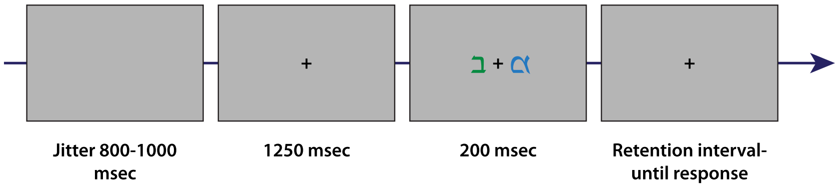

FIGURE 5 An example of a trial sequence in experiment 2. Each trial started with a blank screen, followed by a fixation, which was presented for 1250 ms. Then, the stimuli appeared on both sides of the screen for 200 ms. After their disappearance, a fixation appeared in the middle of the screen, until the participant responded.

only upright stimuli (0 degrees) either in their mirrored or canonical form.

Importantly, if flip rotation is, indeed, an additional process, that consumes VWM capacity, this should be indicated by a higher CDA amplitude, even without the interaction with the degree rotation. Namely, we used the same mirror image task as in Experiment 1, except that all the letters were presented in their upright form, without plane rotation. Meaning, only flip rotation was required in Experiment 2. Similar to Experiment 1, participants were asked to indicate whether the letter was in its canonical form or mirrored form.

3.1 | Method

The method was the same as Experiment 1, except for the following:

3.1.1 | Participants

The experiment included 20 participants (15 females), ages 18–32 (mean age 23). Two participants were replaced due to rejection rate higher than 30%.

3.1.2 | Stimuli and procedure

The discrimination task is illustrated in Figure 5. The experiment was identical to experiment 1, except for the following: The stimuli were blue or green Hebrew letters (“ת” “פ” “ע” “מ” “ל” “ג” “ב”) presented at their canonical form or in their mirrored form. At the beginning of each trial, a blank screen appeared for 800–1000 ms (with 50 ms increments, the overall presentation duration was determined randomly), followed by a fixation presented for 1250 ms. Then, two stimuli appeared on both sides of the screen for 200 ms, followed by a fixation, which was presented until a response was received. Participants were asked to recognize whether the letter presented in the target color was in its canonical form or in its mirrored form. The experiment included 60 practice trials and 8 experimental blocks, each block had 60 trials.

3.1.3 | Electrophysiological recording and processing

CDA

Stimulus-locked. The continuous data were epoched from −200 ms from stimulus onset to 650 ms. Artifact detection was performed on a −200 ms until 650 ms window relative to stimulus onset. This procedure resulted in a mean rejection rate of 6.42%. Statistical analysis was performed on a 400–650 ms window.

Response-locked. The continuous data were epoched from −700 to 200 ms relative to the response. Artifact detection was performed on a −700 ms until 0 ms window relative to the response. RTs shorter than 300 ms were removed from the analysis. This procedure resulted in a mean rejection rate of 7.37%. Statistical analysis was performed on a −300 to 0 ms window.

N2pc

The analysis was similar to the CDA stimulus-locked analysis. Statistical analysis was performed on a 150–250 ms window.

3.2 | Results

3.2.1 | Behavioral results

The average accuracy rate was 96.6%. Detailed accuracy for each condition can be found in Appendix D.

RTs in exp. 2

RT results are presented in Figure 6. One-way ANOVA was conducted with the Letter (Canonical vs. Mirrored) as a variable. There were longer RTs for the Mirrored condition ($F(1, 19) = 7.17$, $p = .015$, $\eta_p^2 = 0.27$), reflecting the added flip rotation process, since the only difference

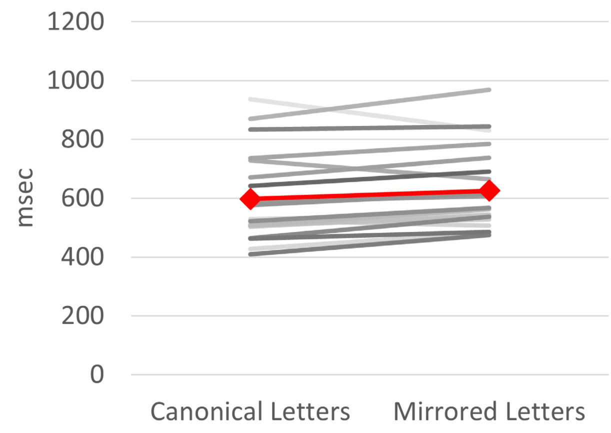

FIGURE 6 RTs in ms for experiment 2.

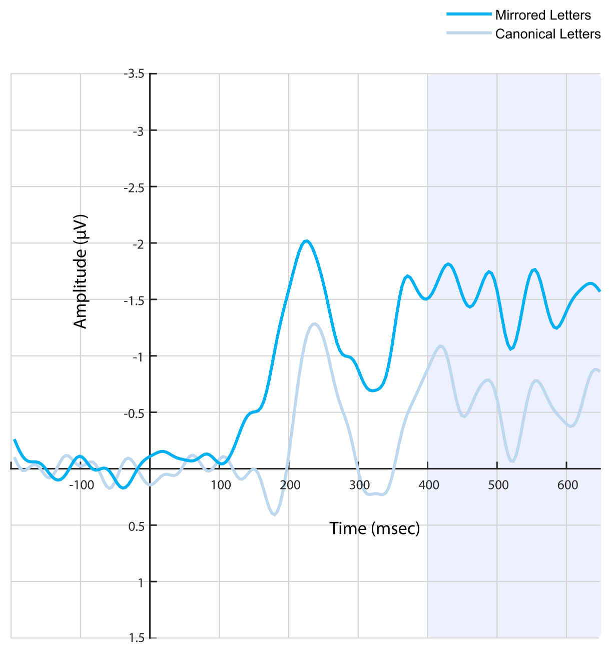

FIGURE 7 CDA amplitude for experiment 2, stimulus-locked. The amplitude is an average of the electrodes P7, P8, PO3, PO4, PO7, and PO8. The colored rectangle marks the time window analyzed for the CDA: 400–650 ms relative to stimulus onset. The same electrodes were analyzed for the N2pc as well, in a 150–250 ms window.

between the conditions was the canonical versus mirrored presentation.

We observed here faster RTs in Experiment 2, even though the stimuli were identical to Experiment 1 (876.8 ms in Experiment 1 vs. 611.6 ms in Experiment 2). This suggests that the performance of flip rotation was, indeed, influenced by the presence of rotation on the page plane in the task. The inclusion of the other degree conditions slowed down the flip rotation process in Experiment 1 even when plane rotation was not needed. Nevertheless, we observed that the flip rotation alone was still more difficult than maintaining the information, even without the interaction with the degrees rotation.

3.2.2 | Stimulus-Locked CDA amplitude in exp. 2

CDA results are presented in Figure 7. Results showed a higher CDA amplitude for the Mirrored condition ($F(1, 19) = 28.01$, $p < .001$, $\eta_p^2 = 0.60$), indicating more VWM involvement when performing a flip rotation than when maintaining the object alone. This suggests that flip rotation requires additional VWM involvement even without the context of plane rotation in the task.

3.2.3 | Response-Locked CDA amplitude in exp. 2

CDA results are presented in Figure 8. Results showed a higher CDA amplitude for the Mirrored condition ($F(1, 19) = 27.40$, $p < .001$, $\eta_p^2 = 0.59$), supporting the stimulus-locked results, which suggested more VWM involvement when performing a flip rotation than when just maintaining the object.

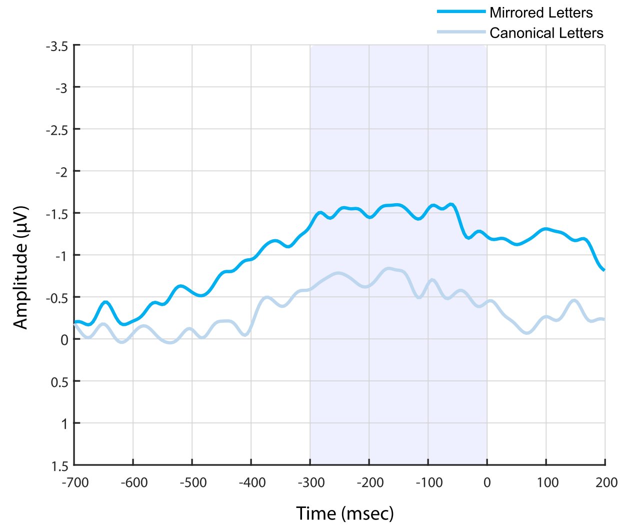

FIGURE 8 CDA amplitude for experiment 2, response-locked. The amplitude is an average of the electrodes P7, P8, PO3, PO4, PO7, and PO8. The colored rectangle marks the time window analyzed for the CDA: −300 to 0 ms relative to the response.

3.2.4 | Post-Hoc analysis: N2pc

N2pc results (see Figure 7) showed a higher N2pc amplitude for the Mirrored condition ($F(1, 19) = 45.92$, $p < .001$, $\eta_p^2 = 0.71$). This is in line with the main effect for the condition we observed in Experiment 1.

In Experiment 2, we observed that flip rotation behaved somewhat differently without the presence of rotation on the page plane in the task (e.g., the differences in RTs). However, the results showed that the flip rotation still taxed VWM more than just the maintenance of the same visual information.

3.3 | Discussion

In this study, we examined whether there are two types of rotations involved in the classical mirror image task. To that end, we focused on the load they impose on VWM.

Our results showed several differences between the two types of mental rotation regarding VWM involvement, as indicated by the CDA. In Experiment 1, we observed a degree effect only in the trials, which did not demand flip rotation. Trials that involved flip rotation only showed a difference between conditions that required performing two rotations (flip rotation and 60, 120, or 180 degrees rotation) and the 0 degrees condition that required only one rotation (flip rotation). Thus, adding the flip rotation seemed to cause a substantial load to VWM: once we have both types of rotations we can no longer differentiate between the degrees.

One option is that the differences we found between the degrees could be related to the duration of the maintenance stage in VWM, as suggested by Prime and Jolicoeur (2010). Namely, when an object is no longer maintained in VWM, the CDA amplitude decreases, and therefore there might be differences in amplitude, simply because in one condition an item is still maintained at a specific time point, whereas in the other condition, the item is no longer maintained in VWM. Indeed, we did observe some differences in offset latency between the conditions, replicating Prime and Jolicoeur (2010). However, we observed differences in the response-locked CDA amplitude as well. The response-locked analysis is not influenced by the offset differences between the conditions. Thus, finding amplitude differences in the response-locked analysis is strong evidence for greater VWM involvement across the degrees conditions.

Experiment 1 results showed no difference between the 180 degrees and the 120 degrees in the canonical trials. These results can suggest that the VWM capacity limit is reached already at 120 degrees of rotation. Reaching the capacity limit in the CDA analysis could explain why we found an interaction in the CDA results but not in the RT results. The CDA reflects VWM capacity limits, such that its amplitude can rise only until a certain point. When the stimulus was mirrored the CDA amplitude reached its limit and did not continue to rise with the increase in the degree of rotation. However, since we did not limit the time of response, RTs could rise, reflecting the increase in difficulty as the degree of rotation increased.

In Experiment 1, we observed an interaction between the Letter and the Degrees in the CDA amplitude, as well as the main effect for Letter in the RTs. In Experiment 2, we observed flip rotation without the context of rotation on the page plane. Experiment 2 showed that the flip rotation taxed VWM more than just maintaining the same information, even when performed without the rotation on the page plane conditions.

In addition to the VWM results, we have also found early attentional differences in the N2pc component, which reflects an early attention process and has been suggested to be connected to attentional engagement (e.g., Zivony et al., 2018). Our results showed a pattern of an increased negative amplitude when the letter had an angle compared to when it was presented at 0 degrees, which can be interpreted as requiring more attentional engagement when the letter is presented with an angle (Zivony et al., 2018), or as an increase in task difficulty (Drisdelle & Jolicoeur, 2018). Overall, we observed differences between the rotation type (main effect for Letter) and between the degrees conditions (main effect for Degrees), but the lack of interaction points to a different pattern than the one observed in the CDA amplitude analysis. Those results suggest a difference in the attentional engagement required for each of the rotation types. Those differences were found in a post-hoc analysis and further research is required to better understand them.

Our results support the need to differentiate between two types of rotations when analyzing mental rotation tasks. When performing the classic task described here, most studies overlooked the difference between the two types of rotation, choosing instead to categorize their results solely by degree conditions. Nevertheless, there are a few articles that identified the difference between the two types of rotations and suggested that the two types of rotations happen sequentially, when the flip rotation is performed after the rotation on the page plane. It has been claimed that both rotations are required for the mirrored/canonical judgment (Hamm et al., 2004; Núñez-Peña & Aznar-Casanova, 2009). Our findings support the existence of two types of mental transformations involved in letter-rotation tasks of the type examined here: a rotation on the page plane and a flip rotation (e.g., Hamm et al., 2004). Complementing the results of Hamm et al. (2004) we here additionally examined the involvement of a more specific mechanism, namely VWM (see also Prime & Jolicoeur, 2010), and showed that the differences between the two types of rotations influence the amount of information held in VWM. Finally, we observed the first indication of early attention-related differences between the rotation types at play (in terms of the main effect of rotation type on the amplitude of the N2pc component). The importance of analyzing the rotations separately is because of the possibility that the results observed in an experiment using the mirror judgment task are biased: they might be derived from only one of the rotations and not both, or that the manipulation affected one of the rotations in a different way than the other. Future research should address each rotation separately.

3.3.1 | Visual Working Memory and the Contralateral Delay Activity

The CDA is an established marker for VWM activity. Importantly, this means that the CDA should be observed in any task that involves VWM processing. Numerous studies confirmed this argument by finding CDA activity in tasks other than change detection or in situations in which the stimuli remained visible on the screen (see Balaban & Luria, 2020 for a review). For example, a CDA amplitude was present in a change-detection task when the objects remained within view, so without any retention interval (Tsubomi et al., 2013). Moreover, the CDA was present in visual search tasks, multiple objects tracking (MOT) tasks, temporal chunking, and grouping tasks (Akyürek et al., 2017; Balaban & Luria, 2020; Drew et al., 2011; Drew et al., 2018; Hilimire et al., 2011; Luria & Vogel, 2011; Poncet et al., 2016; Reinhart et al., 2016; Reinhart et al., 2019; Schneider et al., 2018; Williams & Drew, 2020). In all these examples, the CDA was observed without a retention interval, as long as VWM was involved. Thus, we argue that the CDA is a valid marker for VWM involvement in any task.

Our results hold importance regarding VWM research as well. The amount of visual information presented was similar between conditions. In both experiments, only one object was presented on the relevant side of the screen. Nevertheless, there were clear differences in VWM load (as reflected by the CDA) that are related to the rotation processes. As we mentioned earlier, VWM is involved even when the objects are still within view, and the CDA component is present as well (Tsubomi et al., 2013). Our results indicated that VWM load is sensitive to the type and number of manipulations we perform on visual objects while maintaining them in VWM. Currently, there is no direct evidence that the CDA amplitude is modulated by the amount of processing that VWM performs.

Previous research looking into online processing investigated paradigms such as the MOT (Drew et al., 2011), updating (Kessler & Meiran, 2008), grouping (Luria & Vogel, 2014; Peterson et al., 2015) and visual search (Hilimire et al., 2011; Jolicœur et al., 2008; Luria & Vogel, 2011). Tasks such as the MOT task, require changing the spatial information that is being stored in VWM following the targets' movement. In visual search tasks, the information that is being stored in VWM is changing throughout the trial, when comparing the distractors to the target template (Hilimire et al., 2011; Luria & Vogel, 2011). While there is certainly "processing" going on (e.g., comparison with the target temple), the representations within VWM remain unchanged. Mental rotation is unique in the sense that the representation itself is manipulated online. Thus, the CDA amplitude rise in previous studies (including MOT and visual search) could be attributed to an increase in the number of items (or item information) stored in VWM or to spatial updating, which is different from mental rotation. Thus, our results presented evidence that the CDA is sensitive to processing difficulty.

However, a second possibility is that the CDA does not represent the actual processing of rotating an object. Rather, we propose that during the rotation process, we create intermediate products (as suggested by Cooper, 1976) and maintain them. Our results showed that the CDA rises with increasing the amount of rotation. The additional load we observed on VWM might be a result of maintaining those discrete steps. When the degree of rotation is higher, more intermediate products are created until we reach the capacity limit. This could be the explanation for the lack of differences between the 120 degree condition and the 180 degree condition. In addition, in the flip rotation, it is possible that we maintain the original form of the object, as well as the updated form, after the flip rotation. Maintaining both objects might be the reason for the increase in the CDA amplitude. Further research is needed to establish this theory.

3.3.2 | Conclusions

To conclude, we demonstrated that there are at least two types of fundamentally different mental rotations, which tax VWM differently and engage attention differently. We recommend that in the future those rotations will be analyzed separately in every mental rotation task, which includes both. In addition, we have presented evidence that the CDA reflects rotation difficulty when processing just one item.

AUTHOR CONTRIBUTIONS

Maya Ankaoua: Conceptualization; formal analysis; investigation; methodology; project administration; software; visualization; writing – original draft; writing – review and editing. **Roy Luria:** Conceptualization; funding acquisition; resources; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST

The author declares that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Open Science Framework at https://osf.io/ueb6n/.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A-D Supplementary material.

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