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Age-associated Delay in Mental Rotation

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Abstract

Age-associated slowing in mental rotation (MR) process has been documented in the literature. Particularly, the intercept of the response times (RTs) function of rotation angle has been consistently found to be larger in older than in younger adults. However, the intercept represents the speed of response in two distinct sub-processes of MR: the initial phase of stimulus encoding and the final phase of response selection and execution. Thus, it remains unclear which of these two sub-processes of MR is affected by age. To investigate this, we recorded event-related potentials in younger and older individuals during a letter rotation task. The onset of the rotation-related negativity (RRN), the electrophysiological correlate of MR, was delayed in older (n = 20; mean age = 20.1) as compared to younger participants (n = 20, mean age = 73.4). Consistent with this observation, additional analyses revealed that the RRN amplitude was modulated by rotation angle between 350 and 500 ms post-stimulus in younger adults (n = 26, mean age = 21.0), while this modulation only emerged in the later time window (500-650ms) in older participants (n = 26; mean age = 73.6). These results suggest that MR occurs later in older adults and demonstrate that the initial phase before MR proper is one source of the age-related slowing observed in MR tasks. Possible accounts for this age-associated delay include a prolonged phase of stimulus encoding and/or selective difficulties in directing attention away from the external stimulus towards its internal mental representation.

Key words: mental rotation; aging; onset; RRN; delay

Introduction

Mental rotation (MR), one of the most widely used assessment for visual mental imagery, refers to the human ability to represent an object and mentally rotate it in the mind's eyes. In a classic MR task, first introduced by Shepard and Metzler (1971), participants are asked to compare two stimuli to determine whether they are identical or mirror images of one another. Typically, one of the stimuli is rotated (between 0 and 180 degrees on different trials; e.g. Shepard & Metzler, 1971) and response times increase linearly with increased rotation angles between the stimuli. This has been interpreted as evidence for a dynamic mental imagery process based on a visual representation of the stimulus akin to its actual physical rotation (Shepard & Metzler, 1971; Shepard & Cooper, 1982). It has been suggested that this dynamic process contains at least three functionally independent sub-processes: (a) perceptual encoding and discrimination of the stimuli, (b) pure MR process, (c) response selection and execution. Empirical evidence suggests either that these sub-processes are organized in a strictly sequential manner (Stoffels, 1996) or that consecutive processes do overlap but only to a very small extent (Heil, 2002).

The effect of aging on MR has been investigated in a number of behavioural studies (e.g., Berg, Hertzog, & Hunt, 1982; Cerella, Poon, & Fozard, 1981; Dror & Kosslyn, 1998). Similar to younger individuals, RTs in older adults increase linearly with rotation angle. Some studies have suggested that these linear increases of RTs as a function of rotation angle are characterised by steeper slopes in older compared to younger participants. Because the slopes derived from the RT function of rotation angles reflect the central phase of MR, representing how quickly the mental representation of the object can be rotated in the mind's eyes (MR rate), these findings suggest the presence of an age-associated slowing of the MR rate (Cerella, Poon

& Fozard, 1981; Gaylord & Marsh, 1975). However, other studies have failed to observe these age-associated slope differences (e.g. Jacewicz & Hartley, 1979). This inconsistency, at least partly, could be explained by the different age groups considered in different studies (e.g., the age range of older participants was 66-77 in Cerella, Poon & Fozard, 1981, but was 53-62 in Jacewicz & Hartley, 1979). In addition, Just and Carpenter (1985) suggested that the age-associated slowing in the slope measure may be explained by the different strategies selected by younger and older adults. Therefore, the question of whether there are age-related slowing in MR rates remains open.

The analysis of the RTs functions of rotation angle has consistently shown the presence of larger intercepts for older as compared to younger individuals (Dror & Kosslyn, 1994; Saimpont, Pozzo & Papaxanthis, 2009; Thomas, 2016). The intercept represents the speed of responses in two distinct cognitive processes, the identification of the stimuli and the execution of the responses (Cooper & Shepard, 1973; Just & Carpenter, 1976). Thus, it remains unclear which of these two cognitive sub-processes of MR is affected by ageing. The presence of an age-associated slowing in the generation of motor-responses has been well documented in the literature (Falkenstein, Yordanova, Kolev, 2006; Roggeveen, Prime & Ward, 2007). In addition, evidence suggests that one source of age-associated slowing is related to post-rotation process (e.g. parity judgement or response execution) (Hertzog and Rypma, 1991). Based on these evidence it is likely that the selection and execution of the correct response after stimulus rotation takes longer in older than younger adults in MR tasks. However, it is possible that in addition to the age-related slowing of response selection and execution, older adults are slower during the initial stimulus encoding phase before the onset of MR.

Electrophysiological measures have been used to characterise the time course of the process associated with MR. ERP studies investigating the neural mechanism of MR have primarily used familiar stimuli (e.g. letters or digits). Typically, in these ERP studies one letter is briefly presented on the screen in one of two possible versions (standard vs mirrored) and with different rotation angles. In order to perform the letter version judgment, participants are assumed to complete an "orientation–identicalization" process (Heil, 2002) in which the stimulus representation is mentally rotated in a continuous way until it can be aligned and compared to its canonical representation stored in memory. The analyses of ERPs elicited by both standard and mirror stimuli have shown the presence of a slow negative-going ERP component between 350 and 650ms post-stimulus onset which is maximal over parietal electrodes (e.g. Núñez-Peña & Aznar-Casanova, 2009; Núñez-Peña, Aznar, Linares, Corral, & Escera, 2005, Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989). This rotation related negativity (RRN) is sensitive to the rotation angle of the stimuli because its amplitude becomes more negative with increased rotation angles (for a review see Heil, 2002). Over the past 30 years, the RRN has been used as a tool to investigate the cognitive processes underlying MR. For example, the onset of the RRN was found to be delayed when the perceptual quality of the stimulus was deteriorated or when the stimulus was more difficult to discriminate (e.g., Heil and Rolke, 2002). Thus, when the initial encoding phase took longer, the onset of the RNN was delayed. Therefore, they suggested that the onset of RRN could be used as a temporal marker for the onset of the pure MR process.

To investigate the effect of age on MR, we compared directly the time course of the MR processes in younger and older individuals. Electrophysiological and behavioural measures were recorded during a classic letter rotation task (e.g. Hamm, et al., 2004; Heil, 2002) in which participants reported the standard or mirrored version of a character presented on the screen. If older adults are slower than younger participants in encoding the stimuli during the initial processing stage, the following stage - mental rotation proper - should be delayed in this age group. This should be observed in both behavioural and ERP measures and specifically reflected by larger intercepts in the RT function of rotation angles as well as an age-associated delay in the onset of the RRN for older than younger participants.

Method

Participants

Twenty-six younger (13 women; age 18-29 years, mean = 21.0, standard deviation = 2.9) and twenty-six older adults (13 women; age 66-79 years, mean = 73.6, standard deviation = 4.5) were recruited in this experiment. All of them reported no history of neurological disorders and gave written informed consent to participate in the study after the nature of the study had been explained to them. The study was approved by the Psychology committee in University of Edinburgh.

Stimuli and Procedure

Participants were seated in an electrically shielded, dimly lit, sound attenuating room. The computer monitor was located at a distance of 76cm 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. The letters presented in white on a black background (height: 3 cm, 2.26° of visual angle). These letters were presented in a canonical way (standard 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° (6 rotation angles). Stimulus rotation followed two different directions clockwise or counter-clockwise from the vertical upright position of the stimuli.

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 a standard or mirrored version. Each block included 96 trials (4 letters × 2 stimulus type × 6 rotation angle × 2 orientation of the rotation) presented in random order. Each participant completed ten blocks.

During EEG recording, participants were instructed to keep their eyes on the fixation presented on the screen and their index fingers on the two keys on the response box, which was vertically arranged in front of them. The top button was set for responses to standard stimuli and the bottom 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 begun, participants completed a training block of 48 trials to familiarise with this MR task. Here, the letters “G” and “J” were used which were not included in the set of experimental stimuli.

Electrophysiological Recording and Analysis.

EEG was recorded using a Biosemi recording system from 64 active electrodes (Fpz, Fp1, Fp2, AFz, AF7, AF3, AF4 AF8, Fz, F7, F5, F3, F1, F2,F4, F6, F8, FCz, FT7, FC5, FC3, FC1, FC2, FC4 FC6, FT8, Cz, T7, C5, C3,C1, C2, C4, C6, T8, CPz, TP7, CP5, CP3, CP1, CP2, CP4, CP6, TP8, Pz,P9, P7, P5, P3, P1, P2, P4, P6, P8, P10, POz, PO7, PO3, PO4, PO8,Oz, O1, O2, Iz) positioned on the scalp according to the 10/20 system at a sampling rate of 512 Hz. Two additional electrodes positioned on the left and right ear lobes served as references. Horizontal and vertical EOG were measured unipolarly from four additional electrodes, two placed on the outer canthi of the eyes (hEOG) and two over the suborbital and the supraorbital ridges of the right eye (vEOG), respectively.

The Brain Vision Analyzer software (BrainProducts GmBH, Germany; version 2.1.2) was used for the offline analysis of the EEG data. The EEG signal was digitally re-referenced to the average of the left and right reference electrodes. VEOG and HEOG were calculated offline as the difference between top and bottom VEOG electrodes and left and right HEOG electrodes, respectively. EEG, hEOG and vEOG were filtered using a 0.53 high pass and a 40 Hz low pass filter and segmented into discrete, single-trial epochs. As discussed below two different statistical analyses were carried out on the amplitude and latency of the RRN components measured in the two groups.

For the *latency analysis* (jackknife-based method, see below), longer epochs (from -100ms to 900ms post stimulus onset) were used to capture both the onset and offset of the RRN components in both age groups. These longer epochs contained an increased number of artefacts because they tend to occur towards the end of the trial (when participants respond). Ocular artefacts caused by vertical eye movements (blinks) were corrected with the Gratton-Coles-Algorithm (Gratton, Coles, & Donchin, 1983). Remaining artefacts were rejected using an amplitude criterion (EEG amplitudes exceeding ±80 μV at any scalp electrodes). Six older participants with a low signal-to-noise ratio (< 50% trials left in any experimental condition) were excluded from the jackknife analysis. Thus, 20 participants were included in the older participants group (8 women; age 68-78 years, mean = 73.4, standard deviation = 4.4). To keep the sample size equal across age groups, the first 20 younger adults (11 women; age 18-24 years, mean = 20.1, standard deviation = 1.3) recruited in this study were selected for this comparison.

For the *amplitude analysis*, we used shorter 750ms long epochs (from 100ms before to 650 ms after letter onset). Trials with eye blinks (VEOG exceeding ± 60 μV), horizontal eye movements (HEOG exceeding ± 80 μV) and other artefacts (EEG amplitudes exceeding ±80 μV at any scalp electrodes) throughout the epoch were excluded from analysis. Because these shorter segments included less artifacts, individual ERP averages had a better signal-to-noise ratio and all the 26 younger (age 18-29 years, mean = 21.0, standard deviation = 2.9)) and 26 older participants (age 66-79 years, mean = 73.6, standard deviation = 4.5) were included in these analyses

In both analyses, individual averages were first computed for each participant. ERPs to visual stimuli were averaged relative to a 100ms pre-stimulus baseline for all combinations of stimulus parity (standard, mirror) and rotation angle (0°, 30°, 60°, 90°, 120°, 150°). Data from trials with different letters (F, L, P and R) and different directions of rotation (clockwise, counter-clockwise) were collapsed across. Only trials with correct responses were included in these ERP averages.

RRN Latency analysis (jackknife-based method)

To directly investigate the presence of age differences in the time course of the RRN, the jackknife-based method (Miller, Patterson, and Ulrich, 1998) was used to measure latencies differences in the two age groups. Because differences in latency estimates obtained from the grand averages are less variable than those obtained from individual-subjects, the jackknife method estimates the standard errors of the grand-average latencies through an iterative procedure in which averages are computed from subsamples in which a different participant is excluded from the original sample each time (Miller, Patterson, and Ulrich, 1998; Ulrich & Miller, 2001). In line with existing literature in which the jackknife-based method was applied to the RRN component (Heil & Rolke, 2002), the RRN was computed by subtracting the ERPs elicited by the 30° condition from the waveform elicited by the 150° condition, separately for standard and mirror letters. Latency differences were estimated by examining when the RRN amplitudes for each stimulus type and each age group reached 50% of its maximum amplitude. Independent t-tests were used to compare latencies differences across age groups with corrections suggested for the jackknife-based scoring in factorial design (Ulrich & Miller, 2001).

RRN Amplitude analysis

To detect possible differences between the MR processes in the two age groups, the average amplitudes of the ERP waveforms were computed within two consecutive time windows based on the early and late phase of the RRN component (350-500ms and 500-650ms, respectively). ERP studies of MR have shown that the amplitude of the RRN component increases linearly with increasing rotation angles (Heil & Rolke, 2002; Núñez-Peña et al., 2005; see Heil, 2002, for review). Based on existing literature on younger individuals we expected to observe MR processes in both the 350-500ms and 500-650ms time windows as indexed by main effects of rotation angle described by linear trends. If older participants show a delay in MR processes, this should be reflected by linear increase of the RRN as a function of rotation angle in the 500-650ms but not in the 350-500ms time window.

In line with previous studies (e.g. Quan, Li, Xue, Yue & Zhang, 2017) ERPs were quantified at central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) where the RRN has been shown to be maximal. Consistent with existing literature (Kartzman & Terry, 1983; Picton, Stuss, Champagne & Nelson, 1984), ERP amplitudes were smaller in older as compared to younger participants (a main effect of age was evident in the 350-500ms and 500-650ms time windows - all Fs $(1, 48) > 5.38$, all ps $< .025$, all $\eta_p^2 > .10$). This amplitude difference between the younger and older individuals may represent some physical difference in skull-thickness (Picton et al., 1984). Thus, to avoid possible confounds driven by the this general ERP difference across groups, ERP analyses were carried out directly on the amplitudes of the RRN components calculated by subtracting ERPs elicited on the non-rotation trials (0°) from ERPs elicited on different rotation angles trials (30°, 60°, 90°, 120°, 150°) in the corresponding conditions.

For each of the time windows considered, statistical analyses of the ERP mean amplitudes were conducted with mixed ANOVAs with age (younger or older) as between-subject factor as well as stimulus type (standard or mirror) and rotation angle (30°, 60°, 90°, 120°, 150°) as within-subject factors.

Behavioural Analysis

In all the analyses presented below, the data from the same orientation clockwise and counter-clockwise were combined. RTs exceeding two standard deviations above or below the mean calculated separately for each experimental condition and each participant were excluded from the analyses (4.8% of the trials on average). Mixed ANOVAs were carried out on both mean accuracy rates and mean response times[1] (RTs, calculated over correct trials only) with stimulus type (standard or mirror) and rotation angle (0°, 30°, 60°, 90°, 120°, 150°) as within-subject factors and age (younger or older) as between-subject factor[2]. To fully characterise the

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[1] As requested by one anonymous reviewer, the RT analysis was also carried out on the within-participant median RTs. Analogous results were observed in both median and mean RT analyses.

[2] Although no sex difference has been reported in the literature during the MR of characters (Jansen-Osmann & Heil, 2007), preliminary analyses were carried out including the factor gender. Results revealed no effect of gender in the behavioural analyses and no interaction between gender and the factors of interest in the ERP analyses. Thus, the factor gender was not included in the final analyses.

cognitive processes underlying MR, whenever significant main effects or interactions involving the factor rotation angle were observed, trend analyses were carried out to calculate the estimated slopes and intercepts in the RTs as a function of rotation angle. In these cases, additional ANOVAs were carried out on the estimated slopes and intercepts to further investigate the rate of MR or the time needed to encode stimuli and to respond, respectively, for different stimulus types or in different age groups.

Results

Response Times

The RT analysis revealed a main effect of *rotation angle*, F (1.6, 81.4) = 250.98, $p <$ .001, $\eta_p^2 = .83$. RTs linearly increased with increasing rotation angles, F (1, 50) = 325.69, p < .001, $\eta_p^2 = .78$. In addition, there was a main effect of *stimulus type*, F (1, 50) = 200.17, p < .001, $\eta_p^2 = .80$, with longer RTs in the mirror condition (M = 836.6ms, SD = 199.2) as compared to the standard one (M = 720ms, SD = 157). The ANOVA also yielded a significant *stimulus type* × *rotation angle* interaction, F (2.7, 133.8) = 7.30, $p < .001$, $\eta_p^2 = .13$. Separate analyses carried out for each stimulus type showed significant main effects of rotation angle for both standard (F (1.7, 87.1) = 261.62, $p < .001$, $\eta_p^2 = .84$) and mirror letters (F (2.0, 100.8) = 121.50, $p < .001$, $\eta_p^2 = .71$). RTs and rotation angles were linearly related in both cases (both Fs >= 166.61, ps < .001, η_p^2 >= .77). As shown in Fig.1, the rate of mental rotation (slope) was slower for mirror letters (mean = 1.7ms/degree, SD = 0.8) than standard ones (mean = 2.0ms/degree, SD = 0.9), F (1, 50) = 4.18, $p = .046$, $\eta_p^2 = .08$. Furthermore, a larger intercept, F (1, 50) = 88.12, $p < .001$, $\eta_p^2 = .63$, was present for mirror (mean = 579.6ms, SD = 178.1) than standard letters (mean = 712.9ms, SD = 123.2).

The main effect of *age*, F (1, 50) = 39.71, $p < .001$, $\eta_p^2 = .44$, revealed that younger (mean = 662.3ms, SD = 131.3) were faster than the older adults (mean = 894.4ms, SD = 145.4) in this letter MR task. In addition, the interaction between *age* and *stimulus type* emerged to be significant, F (1, 50) = 16.28, $p < .001$, $\eta_p^2 = .25$. Follow-up analyses conducted separately for each age group revealed significant main effects of stimulus type in both younger (F (1, 25) = 44.49, $p < .001$, $\eta_p^2 = .64$, standard = 626.1ms, SD = 22.2; mirror

= 705.4ms, SD = 29.3) and older adults (*F* (1, 25) = 140.16, $p < .001$, $\eta_p^2 = .85$, standard = 822.3ms, SD = 25.6; mirror = 973.6ms, SD = 29.8).

The ANOVA also revealed a significant interaction between *age* and *rotation angle*, *F* (1.6, 81.4) = 11.81, $p < .001$, $\eta_p^2 = .19$. The main effect of rotation angle was present in both younger (*F* (1.5, 38.2) = 108.06, $p < .001$, $\eta_p^2 = .81$) and older participants (*F* (1.6, 41.1) =144.68, $p < .001$, $\eta_p^2 = .85$). RTs followed both linear (both *F*s ≥ 158.48, *p*s < .001, $\eta_p^2 \geq .86$) and quadratic trends (both *F*s ≥ 27.10, *p*s < .001, $\eta_p^2 \geq .52$) with rotation angles in each age group. Additional analyses revealed that the MR rate was slower in older participants as compared to younger ones (older: M = 2.1ms/degree, SD = 0.8; younger: M = 1.4ms/degree, SD = 0.6), *t* (50) = -3.82, $p < .001$. In addition, a larger intercept was observed in the older than in the younger (older: M = 725.3ms, SD = 133.1; young: M = 567.2ms, SD = 108.5), *t* (50) = -4.69, $p < .001$, suggesting that older individuals spent more time either encoding the stimuli or making decisions.

No other main effect or interaction was statistically significant. However, as we aimed to explore the performance of younger and older adults in MR in each experimental condition, the intercept of RTs function was further analysed with a mixed ANOVAs with stimulus type (standard vs. mirror) as a within-subject factor and age (younger vs. older) as a between-subject factor. An interaction between *age* and *stimulus type* was found, *F* (1, 50) = 8.37, $p = .006$. Main effects of *age* were present in both standard (*t* (50) = -4.788, $p < .001$) and mirror conditions (*t* (50) = -5.493, $p < .001$). In the standard condition, older adults (M = 647.43ms, SE = 20.7) spent about 140ms longer on non-rotation processes as compared to the younger (M = 507.32ms, SE = 20.7), whereas in the mirror condition the older (M = 821.51ms SE = 27.9) took around 220ms longer than younger participants (M = 604.69ms, SE = 27.9).

---Insert Figure 1 about here---

Accuracy

No effect of *stimulus type* was present on the accuracy rates, F (1, 50) = 1.23, $p = .273$, $\eta_p^2 = .02$. A main effect of *rotation angle* was observed, F (1.8, 89.6) = 56.67, $p < .001$, $\eta_p^2 = .53$. Accuracy rate decreased with increasing rotation angles (linear trend analysis: F (1, 50) = 71.53, $p < .001$, $\eta_p^2 = .59$). The ANOVA also yielded a *stimulus type* × *rotation angle* interaction, F (1.3, 64.0) = 9.29, $p = .002$, $\eta_p^2 = .16$. Follow-up analyses conducted separately for each stimulus type revealed that the effects of rotation angle were present for both the standard (F (1.3, 63.1) = 38.42, $p < .001$, $\eta_p^2 = .44$) and the mirror letter (F (1.6, 78.1) = 6.11, $p = .007$, $\eta_p^2 = .23$). In both cases, the linear relationship between RTs and rotation angles was confirmed (Fs ≥ 35.06, ps < .011, $\eta_p^2 \leq .58$), with accuracy rates decreasing with increasing rotation angles. This decrement was faster in the standard (mean = -0.1%/degree, SD = 0.1) than in the mirror condition (mean = -0.2%/degree, SD = 0.1), F (1, 50) = 6.25, $p = .016$.

There was no main effect of *age* on accuracy, F (1, 50) = .09, $p > .05$. However, *age* interacted with *stimulus type*, F (1, 50) = 7.45, $p = .009$, $\eta_p^2 = .13$. Follow-up analyses conducted separately for each age group revealed that the older were more accurate to respond to standard letters (mean= 94.2%, SD= 5.2) than mirror ones (mean = 90.9%, SD = 9.7), F (1, 25) = 7.36, $p = .040$, $\eta_p^2 = .16$, but no such difference was found in younger adults (standard = 92.4%, SD = 6.5; mirror = 93.8%, SD = 6.6), F (1, 25) = 3.06, $p > .05$, $\eta_p^2 = .11$.

Moreover, a three-way interaction between *stimulus type, rotation angle* and *age* was present, F (1.3, 64.0) = 4.04, $p = .039$, $\eta_p^2 = .08$. Follow-up analyses conducted separately for each age group revealed a significant *stimulus type* × *rotation angle* interaction in the younger adults (F (1.2, 30.3) = 8.71, p < .001, η_p^2 = .26), but not in the older participants (F (1.4, 35.0) = 1.18, p = .32). For younger individuals, a main effect of rotation angle emerged in standard letters, F (1.2, 30.8) = 22.2, p < .001, η_p^2 = .47, which could be described by both a linear, F (1, 25) = 2.7, p < .001, η_p^2 = .48, and quadratic trend, F (1, 25) = 25.8, p < .001, η_p^2 = .51. However, no such rotation angle main effect was present in mirror letters. Post-hoc analyses with Bonferroni correction revealed that accuracy rates significantly dropped from 90.6% at 120° (SE = 2.1) to 78.5% (SE = .7) at 150°, p =.001, whereas no significant difference emerged between any other two consecutive angles, all ps ≥ .093.

RRN latency analysis (jackknife-based method)

Figure 2 shows the time course of the RRN elicited on standard (*left* panel) and mirror letter trials (*right* panel) measured in younger (black solid line) and older adults (grey dotted line). In this figure the RRN was obtained by subtracting ERPs elicited at 150° from ERPs at 30° (see Heil & Rolke, 2002) pooled over central-parietal sites (CPz, CP1/2, CP3/4, Pz, P1/2, P3/4). A latency shift of the RRN component is visible in older as compared to younger adults for both standard and mirror letter trials.

---Insert Figure 2 about here---

Standard letters

A main effect of *age* was observed on the onset of RRN measured on trials with standard letters, t_c (38) = 11.38, p_c < .001, confirming a systematic delay in the onset of MR processes for older as compared to younger participants (see the left panel in Fig.2; older: M = 490.93ms, SE = 0.4; younger: M = 358.31ms, SE = 0.4)[3]. In addition, also the offset of the RRN elicited on trials with standard letters differed systematically between younger and older adults, as indicated by a significant main effect of age, t_c (38) = 3.40, $p_c < .001$. The offset of MR processes was delayed in the older (M = 739.76ms, SE = 2.97) as compared to younger adults (M = 546.30ms, SE = .40). However, results revealed no significant difference on the duration of the RRN elicited by standard letters in the younger and older adults, t_c (38) = 1.13, $p_c = .13$.

Mirror letters

As depicted in the right panel of Fig.2, a main effect of age was observed on the RRN onset latency, t_c (38) = 2.69, $p_c = .005$. The RRN was delayed in older (M = 543.47ms, SE = 1.37) as compared to younger adults (M = 440.54ms, SE = 1.48). An age-associated delay was (Younger = 621.40ms, SE = 2.22; Older = 896.49ms, SE = 1.00) also observed on the offset of RRN, t_c (38) = 29.16, $p_c < .001$. In addition, the RRN duration on mirror letter trials was significantly longer in older (M = 353.03ms, SE = 1.37) than younger adults (M = 180.86ms, SE = 1.53) (see left panel in Fig.2), t_c (38) = 4.42, $p_c < .001$.

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[3] To test the possibility that this age-related RRN onset delay is associated with differential practice effects in the two age groups, we split the trials into first and second half (blocks 1-5 and 6-10, respectively) for each individual participant and each experimental condition. The RRN was measured by subtracting ERPs elicited in the 30° condition from those elicited in the 150° condition. The jackkniffe procedure was applied to calculate the RRN onset. To test the practice effect, the onset of the RRN components measured in the first and second half of the blocks were directly compared between age groups. The main effect of practice was only observed in the older group in the mirror condition, $t_c(25) = 2.59$, $p_c = .008$. For older participants, the RRN onset was significantly earlier in the second (mean = 522.47ms, SE = .49) compared to the first half of the trials (mean = 563.79ms, SE = .46). However, this practice effect did not emerge in the younger group in both standard ($t_c(25) = .87$, $p_c = .20$) and mirror condition ($t_c(25) = 1.47$, $p_c = .08$), as well as in standard condition in the older ($t_c(25) = .67$, $p_c = .25$). Because earlier RRN components were observed in the second half of the trials in older but not younger individuals, this practice effect should reduce the age-related MR delay observed in the main latency analysis. Thus, the delayed RRN onset in older compared to younger participants cannot be accounted for by practice effects.

RRN amplitude analysis

Figure 3 shows the RRN component computed by subtracting the ERP waveforms elicited in the upright position (0°) from those elicited in each rotation angle (30°, 60°, 90°, 120°, 150°) separately for each stimulus type (standard vs. mirror). In this figure, the RRN pooled over central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) is shown separately for younger and older participants. An age-associated delay in the RRN is visible in all these figures. While RRN amplitudes appears to be modulated by rotation angle in both early (350-500ms) and late (500-650ms) time windows in younger participants, this RRN modulation by rotation angle is only visible in the late time window (500-650ms) in older participants, regardless of stimulus type.

---Insert Figure 3 about here---

Early RRN time window (350-500ms)

A main effect of *rotation angle* was observed in this early RRN time window measured between 350 and 500ms post-stimulus onset (F (2.7, 132.8) = 22.27, $p < .001$, $\eta_p^2 = .31$). Linear trend analyses revealed that the RRN amplitude became more negative with the increasing rotation angles (F (1, 50) = 39.63, $p < .001$, $\eta_p^2 = .44$). In addition, stimulus type was found to interact with rotation angle, F (4, 200) = 16.31, $p < .001$, $\eta_p^2 = .25$. Repeated-measures ANOVAs conducted separately for the different stimulus types revealed the presence of main effects of rotation angles for both standard (F (3, 149.3) = 33.28, $p < .001$, $\eta_p^2 = .40$) and mirror letters (F (3.3, 160) = 3.19, $p = .023$, $\eta_p^2 = .06$). RRN amplitudes and rotation angles were linearly related in both standard (F (1, 50) = 51.34, $p < .001$, $\eta_p^2 = .51$) and mirror conditions (F (1, 50) = 5.62, $p = .022$, $\eta_p^2 = .10$).

The main effect of *age*, F (1, 50) = 5.52, p = .023, η_p^2 = .10, revealed that RRN amplitudes were larger in younger (M = -1.0, SE = 0.2) than older individuals (M = -0.5, SE = 0.2).

Furthermore, there was a significant *age* × *rotation angle* interaction, F (2.7, 132.8) = 15.7, $p < .001$, η_p^2 = .24. Separate analyses carried out for each age group revealed the presence of a main effect of rotation angle in younger participants, F (2.3, 57.6) = 32.64, $p < .001$, η_p^2 = .57. Linear trend analyses in younger participants confirmed that the RRN amplitude became more negative with increasing rotation angles, F (1, 25) = 54.84, $p < .001$, η_p^2 = .69. Significant RTs difference was reliably present between each two consecutive angles, all ps ≤ .06. By contrast, no main effect of rotation angle emerged in older participants between 350 and 500ms (F (2.7, 68.1) = 1.21, p = .31).

There was no significant interaction between *age*, *stimulus type* and *rotation angle*, F (4, 200) = 1.96, p = .10.

Late RRN time window (500-600ms).

Main effects of *stimulus type* (F (1, 50) = 13.41, p = .001, η_p^2 = .21) and *rotation angle* (F (2, 97.9) = 48.78, $p < .001$, η_p^2 = .50) were present between 500 and 650 post-stimulus. RRN amplitudes were more negative in the mirror condition (M = -1.3, SE = 0.1) than in the standard one (M = -0.7, SE = 0.2) and became more negative with the increasing rotation angles (linear trend analysis: F (1, 50) = 71.33, $p < .001$, η_p^2 = .59).

Moreover, the interaction of *rotation angle* and *stimulus type* emerged to be significant, F (2.4, 121.6) = 36.44, p = .01, η_p^2 = .11. The presence of a rotation angle main effect was observed for both standard (F (2.3, 113.4) = 37.07, $p < .001$, $\eta_p^2 = .43$) and mirror letters (F (2, 99.1) = 24.0, $p < .001$, $\eta_p^2 = .32$). Trend analyses confirmed the linear relationship between RRN amplitude and rotation angles for both stimulus types (both Fs ≥ 34.37, ps < .001, $\eta_p^2 \geq .41$).

A significant age × stimulus type interaction (F (1, 50) = 10.35, $p = .002$, $\eta_p^2 = .17$) revealed that enhanced RRN amplitudes were present for older (M = -1.2, SE = 0.2) as compared to younger adults (M = -0.3, SE = 0.2) in the Standard condition (main effect of age, t (50) = -3.0, $p = .005$), while no age effect on RRN amplitudes was observed when participants rotated mirrored stimuli, t (50) = .55, $p = .59$.

In addition, a three-way interaction between *age, rotation angle, and stimulus type* was observed in this late time window (see Fig. 3b), F (2.4, 121.6) = 4.29, $p = .012$, $\eta_p^2 = .08$. Follow-up analyses were conducted separately for each age group. No stimulus type × rotation angle interaction was present in the younger individuals, F (2.3, 57.4) = 1.13, $p = .35$. By contrast, a stimulus type × rotation angle interaction was present in older participants (F (2.4, 60.5) = 9.01, $p < .001$, $\eta_p^2 = .27$). In the standard condition, the RRN amplitudes increased with increasing rotation angles (main effect of rotation angle, F (2, 50.1) = 24.61, $p < .001$, $\eta_p^2 = .50$, described by a linear trend, F (1, 25) = 37.35 $p < .001$, $\eta_p^2 = .60$). RRN amplitudes were significantly larger at 150º as compared to 120º ($p = .006$) and at 120º as compared to 90º ($p = .007$). A main effect of rotation angle was also present in the mirror letter condition in older participants, F (1.8, 44.6) = 9.10, $p < .001$, $\eta_p^2 = .27$ (described by a linear trend, F (1, 25) = 9.69, $p = .005$, $\eta_p^2 = .28$) and significant differences between consecutive degrees were found between 30º and 60º ($p = .044$), and between 60º and 90º ($p = .004$).

Discussion

In the present study, we measured the behavioural and ERP correlates of letters MR in healthy younger and older adults to evaluate possible age differences.

When the RRN components elicited in younger and older individuals were directly compared, systematic differences emerged between age groups. The analyses of the RRN latencies revealed a delay in MR processes, as suggested by the presence of later RRN onsets for older as compared to younger individuals. This delay was further confirmed in the amplitude analyses. In younger participants, the amplitude of the RRN measured between 350 and 500ms post-stimulus (early RRN phase), increased linearly as a function of rotation angle (see Fig. 3a, top panel). This suggests that younger individuals were mentally rotating the stimuli during this time window. By contrast, in older participants, the amplitude of the RRN component was not modulated by rotation angle during the early (350-500ms), although this modulation became apparent in the late time window (500-650ms) (Fig. 3a, bottom panel). Thus, MR processes in older participants were delayed as compared to younger individuals. The analysis of the behavioural data provided converging evidence by showing a larger intercept of the RT functions of rotation angles for older as compared to younger participants. Taken together these findings reveal that MR processes occurred later in older adults.

Interestingly, this age induced delay in mental rotation was present for both standard and mirror stimuli. RRN onset latencies were systematically delayed in older as compared to younger individuals during the rotation of both standard and mirror letters. In addition, RRN amplitudes measured between 350 and 500ms post stimulus increased linearly with increasing rotation angles for both standard and mirror letters in younger but not in older participants (as shown in Fig.3b). This suggests that older participants were not mentally rotating stimuli during the early phase of the RRN. These ERP observation were matched by age differences in the behavioural performance which showed that age induced delays were present for both standard and mirror stimuli, as shown by larger intercepts.

While these observations provide strong converging evidence for a general delay in MR in older as compared to younger participants, it is important to consider the possibility that this difference is simply due to increased variance in older individuals. If the onset time of MR as indexed by the RRN varies across trials, the resulting waveform averaged across these trials could be characterised by a later latency and a smaller amplitude. To rule out this possibility an additional analysis on the RRN onset was carried out in which only fast trials for both age groups were included (RTs for each participants were divided into slow and fast trials based on the median RT calculated separately for each experimental condition)[4]. The RRN onset observed on fast trials was still delayed for older as compared to younger participants. This suggests that variance alone cannot explain the age-associated delay in MR.

Existing electrophysiological evidence has suggested that different mechanisms underlie the rotation of mirror and standard stimuli (e.g. Hamm et al., 2004). Rotating mirror letters might be more difficult compared to the rotation of standard stimuli because an additional rotation in and out of picture plane is needed (Hamm et al., 2004; Nunez-Pena & Aznar-Casanova, 2009). Thus, the rotation of mirror stimuli might start later and take longer (Bajric, Rosler, Heil & Hennighaugen, 1999; Murray, 1997; Nunez-Pena et al, 2009). Results observed

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[4] Grand-averaged RRN waveforms (150°-30°) were calculated based on correct trials in which RT were faster than the median RT for each individual participant in each experimental condition. Consistent with the results of the general RRN latency analysis, the age-associated delay is still evident in both standard, t_c (36) = 8.97, p_c < .001, and mirror conditions, t_c (36) = 3.25, p_c = .0012. The onset of RRN elicited by standard letters was delayed in older (M = 467.7ms, SD = 3.0) than younger adults (M = 339.1ms, SD = 1.75). Similarly, there was an age-associated delay on the RRN onset for trials with mirror letters (younger = 441.6, SD = 4.5; older = 506ms, SD = 1.38).

for both younger and older individuals provide direct evidence for the hypothesis that the mental rotation of mirror stimuli is more demanding than that of standard ones (e.g. to rotate the internal representation not only within but also out of the x-y coordinate plane; Hamm et al., 2004; Nunez-Pena & Aznar-Casanova, 2009; Quan et al., 2017).

It is interesting to note that while latency shifts in the onset and offset of the RRN component in older as compared to younger individuals were present for both standard and mirror letter trials, longer RRN durations in older than younger participants were observed during mirror but not standard letter rotation. Stronger differences between age groups were also observed in the speed and accuracy of responses to mirror as compared to standard stimuli. Taken together these findings suggests that age differences related to the duration of MR processes become more evident during the MR of mirror letters. If the rotation of mirror letters involves two distinct MR processes (within the plane and out of the plane, Hamm et al., 2004; Nunez-Pena & Aznar-Casanova, 2009; Quan et al., 2017), the increased MR duration observed in older participants might be at least in part explained by the higher cognitive demands posed by the rotation of mirror stimuli. Alternatively, it is possible that older adults adopted a response criterion to complete the MR of mirror stimuli. Older adults are more likely to show relatively stable levels of accuracy with decreasing RTs (Hertzog, Vernon & Rypma, 1993). Thus, the longer MR duration observed in older participants could simply reflect a more cautious approach during the rotation of mirror stimuli.

One additional aspect of our results that is worth noting is the age-related difference observed in the RTs slopes, which reveals that the MR rate of older participants was generally slower than that of younger participants. However, this observation is in contrast with the outcome of a previous study whereby no such age-difference was observed (Jacewitz & Hartley, 1979). It is possible that age-related differences in the slopes of RTs become apparent only when the age gap between the groups is large enough (the age range of older participants was 66-79 in the present study, but was 53-62 in Jacewicz & Hartley, 1979).

The aim of the present study was to investigate whether older adults are slower during the initial phase of stimulus encoding before the onset of MR. Overall, our results revealed the presence of a general age-related delay in the onset of MR processes. One possible explanation is that older adults need more time to encode/ identify the stimuli before they can start the MR process. Previous ERP studies have shown that MR processes are delayed either when the perceptual quality of the stimuli is reduced or the stimuli are more difficult to discriminate (Heil & Rolke, 2002). In the present study the stimulus remained on screen for 500ms. That is, the stimulus disappeared well before participants were able to identify its version (as suggested by their reaction times). Under these experimental conditions participants were forced to create a mental representation of the stimulus and to fully rely on it during the following processes of mental rotation and decision making. It is therefore possible that older participants took longer to create this mental representation. It has been shown that working memory plays a relevant role in the maintenance of the mental representation of the letter during the rotation process (Hyun & Luck, 2007) and that it decreases with age (Brockmole, Parra, Della Sala & Logie, 2008; De Beni & Palladino, 2004; Reuter-Lorenz & Sylvester, 2005; Zacks, Lynn & Li, 2000). Thus, older adults might be not as efficient as younger adults in creating the internal mental representation which is the initial step necessary for MR.

While this age-related difference could simply be explained by the extended time necessary to older participants to encode the visual stimulus, it is interesting to note that they started to mentally rotate the stimuli (as indexed by the onset of RRN) only after the stimulus disappeared from the screen. This observation might also suggest that disengaging attention from the external visual stimulus on the screen and directing it internally towards its mental representation was more challenging for older than younger participants. Indeed, recent lines of evidence have demonstrated that older participants find it more challenging to inhibit distracting information as compared to younger participants (Hasher, Zacks, & May, 1999; Clapp & Gazzaley, 2012; Gazzaley, Clapp, Kelley, McEvoy & Knight & D'Espsoto, 2008; Gazzaley, Cooney, Rissman, & D'Esposito, 2005) and that distracting information needs longer to be processed in older than younger participants (Cashdollar, Fukuda, Bocklage, Aurtenetxe, Vogel & Gazzaley, 2013; Clapp & Gazzaley, 2012;Clapp & Gazzaley, 2012; Clapp, Rubens, & Gazzaley, 2010; Fukuda & Vogel, 2009; Gazzaley et al., 2005; Minamoto, Osaka & Osaka, 2010). Interestingly, the impact of external distractions differentially affects performance on tasks with internal, as opposed to external, attentional orientations, with older participants selectively impaired in a mental rotation task during which external auditory irrelevant information was presented (Ziegler, Janowich, & Gazzaley, 2018). Although in the present study the visual stimulus on the screen is task relevant and participants should focus their attention on it, it might create an attentional anchor which older participants might find more difficult to disengage attention from. It is therefore possible that the systematic delay observed in older participants in the present study is not only driven by the increased time needed to create an internal representation of the stimulus but also by their ability to disengage attention from the external stimulus and direct it on its internal representation for the mental rotation process.

In sum, the present ERP study investigated the time course of MR during a letter rotation tasks in younger and older adults. The present findings demonstrated that one source of the age-related slowing observed in previous behavioural MR tasks is linked to the initial phase of MR. Specifically, delayed RRN components were observed for both the standard and mirror letter conditions in the older as compared to younger participants. This finding shows that older participants need longer to start the processes of MR possibly because of a prolonged phase of stimulus encoding and/or selective difficulties in directing attention away from the external stimulus and towards its internal mental representation.

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Figure Captions

Figure 1: Behavioural performance for younger and older adults in the letter rotation task. The left panel depicts the response times (RTs) in younger and older adults in the standard (square) and mirror conditions (triangle). The right panel depicts the accuracy rates in younger (solid line) and older adults (dotted line) in the standard (black) and mirror conditions (grey).

Figure 2: Rotation-related negativity (RRN) obtained by subtracting ERPs elicited at 30° trials from ERPs elicited at 150° pooled across central-parietal sites (CPz, CP1/2, CP3/4, Pz, P1/2, P3/4) in the standard (left panel) and mirror conditions (right panel) separately for younger (black solid line) and older individuals (grey dotted line).

Figure 3: Rotation-related negativity (RRN) calculated by subtracting ERPs elicited on non-rotation trials (0°) from ERPs elicited on trials with different rotation angles (30°, 60°, 90°, 120°, 150°) pooled across central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4). Left panels (Fig. 3a) show the RRN elicited in younger and older participants collapsed across different stimulus types, whereas middle and right panels show the RRN elicited during MR of standard and mirror letters, respectively (Fig.3b).

Figure 1

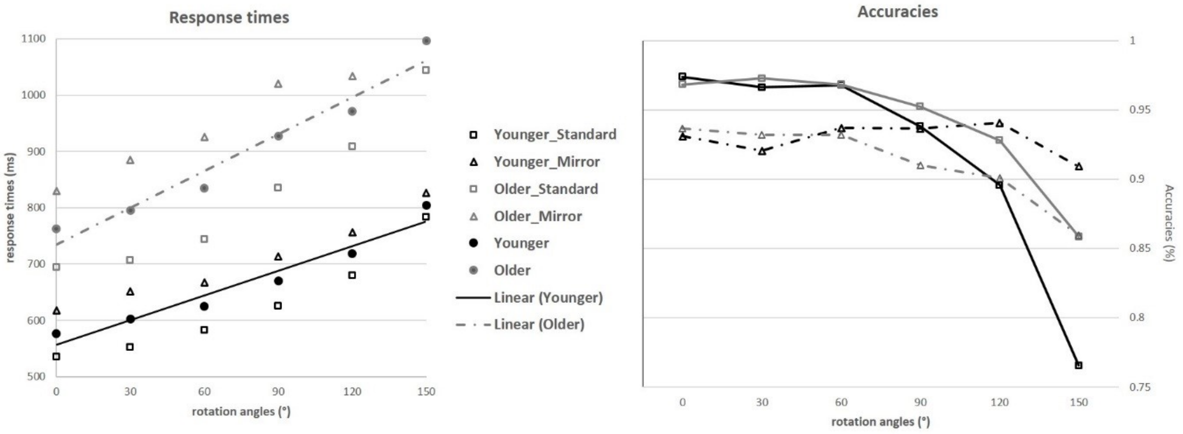

Response times
1100
1000
900
800
700
600
500
response times (ms)
0
30
60
90
120
150
rotation angles (°)
Younger_Standard
Younger_Mirror
Older_Standard
Older_Mirror
Younger
Older
Linear (Younger)
Linear (Older)
Accuracies
1
0.95
0.9
0.85
0.8
0.75
Accuracies (%)
0
30
60
90
120
150
rotation angles (°)

Figure 2

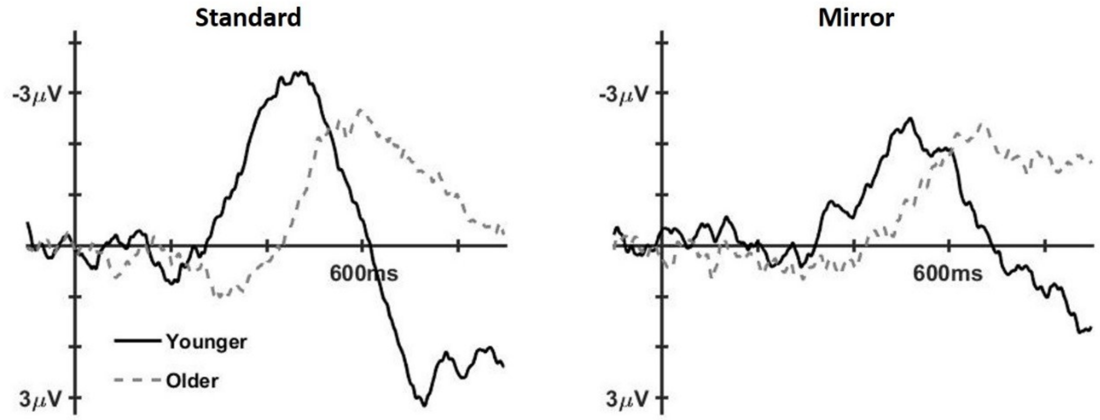
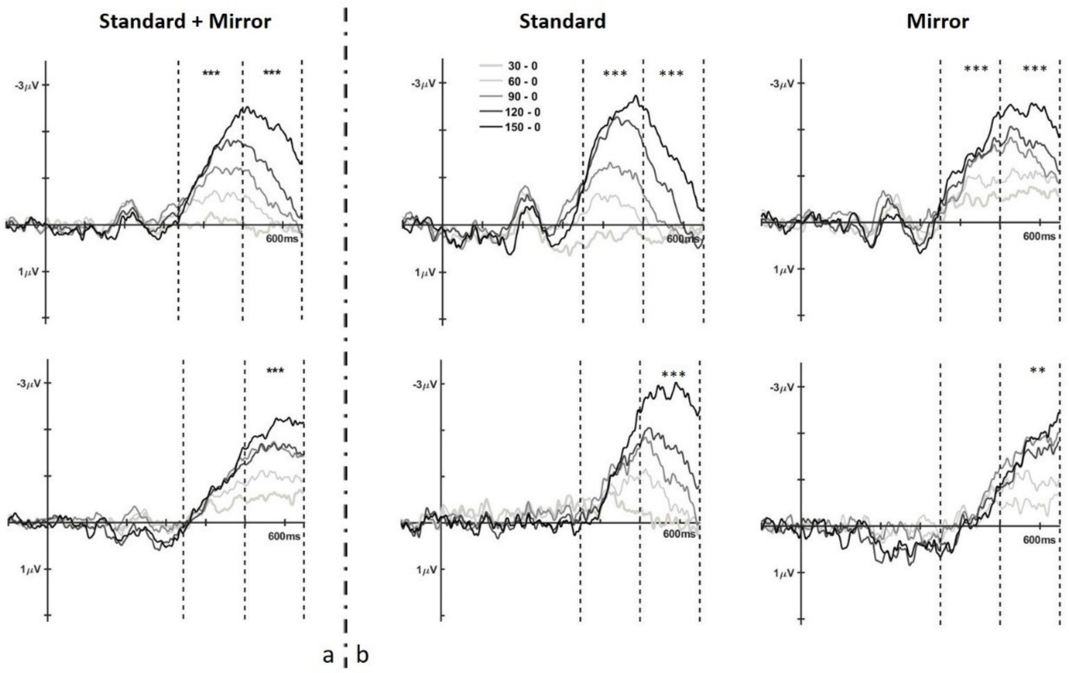


Figure 3


Standard + Mirror
Standard
Mirror
Younger
Older
30 - 0
60 - 0
90 - 0
120 - 0
150 - 0
-3μV
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a
b