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Spatial Transformation in Mental Rotation Tasks in Aphantasia

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Abstract

Aphantasia refers to the inability to summon images to one's own mind's eye, resulting in selective deficits of voluntary object imagery. In the present study, we investigated whether M. X., a case of acquired aphantasia, can still retain some form of spatial transformation processes even though he is unable to subjectively experience voluntary object imagery. M. X. and a group of control participants were asked to complete a letter mental rotation task (MRT), typically used to assess the nature of the spatial transformation, while behavioural and electrophysiological responses were recorded. M. X. was able to complete the MRTs as accurately as controls, showing the pattern of increasing RTs as a function of rotation angle typical of MRTs. However, event-related potentials (ERP) results showed systematic differences between M. X. and controls. On canonical letter trials, the rotation-related negativity (RRN), an ERP component considered as the psychophysiological correlate of the spatial transformation of mental rotation (MR), was present in both M. X. and controls and similarly modulated by rotation angle. However, no such modulation was observed for M. X. on mirror-reversed letter trials. These findings suggest that, at least under specific experimental conditions, the inability to create a depictive representation of the stimuli does not prevent the engagement of spatial transformation in aphantasia. However, the ability to apply spatial transformation varies with tasks and might be accounted for by the specific type of mental representation that can be accessed.

Introduction

Aphantasia, also known as blind imagination, refers to the inability to experience voluntary *object imagery* (Zeman, Dewar, & Della Sala, 2015; Zeman et al., 2020; Dawes, Keogh, Andrillon, & Pearson, 2020). Individuals with aphantasia, which can be an acquired or a congenital condition, cannot form *depictive objects representations* in their minds' eyes in the absence of the corresponding external object or scene (Pearson, Naselaris, Holmes, & Kosslyn, 2015). Although wide variations in imagery vividness had been described over a hundred years ago (Galton, 1880), aphantasia as an imagery generation disorder/deficit only recently has captured scientists' interest (Zeman et al., 2015; Keogh & Pearson, 2018; Keogh, Pearson, & Zeman, 2021). The interest in aphantasia was sparked by the description of the case of M. X., who reported the abrupt loss of his subjective experience of object imagery after he had undergone coronary angioplasty (remodelling of coronary arteries performed from within the arteries) (Zeman et al., 2010). When his object imagery abilities were assessed with the Vividness of Visual Imagery Questionnaire (VVIQ, Marks, 1973, 1995) his scores were significantly lower compared to controls. He performed normally on a wide range of standard tests of perception, visual imagery and visual memory, but showed an unusual pattern of performance in the Brooks' matrix task (1967) and in the classic mental rotation task (MRT) with arm-like cubes (Shepard & Metzler, 1971). In addition, during a face imagery task he showed a different pattern of brain areas activation as compared to controls, with reduced activity in posterior brain areas typically linked to face processing but increased activation in the anterior regions (Zeman et al., 2010).

MRTs are widely used to explore the nature of mental imagery, and specifically the presence of spatial transformation processes[1]. Participants are asked to compare a pair of stimuli presented on the screen at different rotation angles relative to one another to judge whether these are identical or different (Shepard & Metzler, 1971). Typically, response times (RTs) linearly increase with increasing rotation angles (Shepard & Metzler, 1971; analogous findings were replicated in MRTs with different types of stimuli such as arm-like cube objects, e.g., Shepard & Metzler, 1988; character letters, e.g., Cooper & Shepard, 1973). It is assumed that the linear increase in RTs associated with the increasing rotation angles reflects the cognitive manipulation (processing) of the mental representation of the stimuli. According to spatial theories of mental rotation (MR - e.g., Cooper & Shepard, 1973), participants create mental representations that preserves the visual information of the original perceptual stimuli. They then rotate these *depictive representations* in their minds in a MR process considered to be analogous to the physical rotation of the stimuli (spatial transformation processes; Shepard & Metzler, 1971).

When M. X. performed the MRT with arm-like cubes (c.f. Shepard & Metzler, 1971), he was able to complete the task accurately but showed a non-linear pattern of RTs whereas controls showed the typical pattern of increasing RTs as a function of angular disparity. Based on these behavioural results, it was postulated that M. X. completed the MRT using a different strategy compared to controls (Zeman et al., 2010). Indeed, according to his debrief, he attempted to match individual cubes and angles perceptually before responding, using a strategy that did not involve the MR processes based on spatial transformation (Zeman et al.,

[1] We specifically use the term ‘spatial transformation process’ to refer to the mental operations engaged while applying a holistic mental rotation process in processing the stimuli indexed by the rotation-related negativity (RRN) component of event-related potentials (ERPs; e.g., Heil, 2002; Peronnet & Farah, 1989).

2010)[2]. Importantly, because RTs only offer an indirect insight into the strategy adopted by participants during MRTs (e.g., Zhao & Della Sala, 2018; Zhao, Gherri & Della Sala, 2020), it is not possible to ascertain whether M. X. engaged any spatial transformation during the task or whether these were engaged but not modulated by rotation angle in the usual manner. Whether spatial transformation is preserved in individuals with aphantasia in the absence of object imagery is still unclear, though researchers have now started to explore the role of depictive representations in the cognitive processes of individuals with aphantasia by assessing their performance on visual working memory (Jacobs, Schwarzkopf, & Silvanto, 2018; Keogh, Wicken, & Pearson, 2021), spatial memory (Bainbridge, Pounder, Eardley, & Baker, 2021) and autobiographical memory tasks (Monzel, Vetterlein, & Reuter, 2021; Milton et al., 2021).

In the present study, we explored whether the spatial transformation process characteristic of MR can be observed in an individual with aphantasia who cannot voluntarily summon a depictive representation of the stimuli in his mind's eyes. To this aim, we recorded both behavioural and electrophysiological measures while M. X. and matched controls performed a letter rotation task[3] in which one single letter was briefly shown on the screen at different rotation angles. (e.g., Hamm, Johnson & Corballis, 2004; Núñez-Peña & Aznar-Casanova,

[2] This strategy is similar to the one postulated by propositional theories of MRTs (e.g., Liesefeld & Zimmer, 2013), according to which the mental representations of the stimuli are *non-depictive* with stimuli visual information represented in an abstract propositional format (e.g., language-like, descriptive; e.g., Liesefeld & Zimmer, 2013). Thus, in the absence of depictive representations, a*nalytical strategies* can be applied to non-depictive representations to complete the MRT (Cooper, 1975; Cooper & Podgorny, 1976).

[3] The complexity and familiarity of the stimuli used in a MRT are known to affect performance and the strategy used to solve the task (e.g., Sanandaji, Grimm, West, & Sanchez, 2021). The arm-like cubes MRT (e.g., Shepard & Metzler, 1971) used in prior M. X. assessment involved abstract 3D geometrical stimuli characterized by a complex structure (Neubaruer, Bergner, & Schatz, 2010; Sanandaji et al., 2021). The visual complexity of the stimuli together with the fact that the pair of stimuli was displayed on the screen until response may have encouraged the adoption of an analytic strategy by M. X., such as the visual matching of key stimuli features (Shepard & Metzler, 1988). By contrast, in the present study we adopted the classic letter rotation task typically used in ERP studies of MR. In this task, one character letter (either canonical or mirror-reversed) was shown on the screen for a limited period of time (500 ms). Participants had to encode and represent its main features in order to mentally manipulate these after the stimulus disappearance from the screen. Therefore, the letter rotation task chosen in the present study was aimed at encouraging participants to create a mental representation of the visual stimuli.

2009). Participants were asked to report the letter orientation, whether canonical or mirror-reversed. To solve this task using a spatial transformation process, participants must create a depictive representation of the letter in their mind's eye and to rotate it until the letter is upright (0° angle), before they can decide whether it is presented in its canonical or mirror-reverse orientation. Electrophysiological measures have been used to characterise the presence and time course of the MR process in MRTs, thanks to their high temporal resolution. In particular, the rotation-related negativity (RRN) component of event related potentials (ERPs) is considered the electrophysiological correlate of the MR process (for a review see Heil, 2002). The RRN component is elicited over parietal electrodes from around 350 ms after the presentation of the stimulus and its amplitude is sensitive to the stimulus rotation angle, becoming more negative with increasing rotation angles (e.g., Heil & Rolke, 2002; Núñez-Peña & Aznar-Casanova, 2009; Núñez-Peña et al., 2005; Rösler et al., 1995; Wijers et al., 1989). Thus, the presence of the RRN component in a MRT is considered as an indication of the presence of the spatial transformation process associated with MR.

We expected controls to show the typical increments of RTs and RRN associated with increasing rotation angles on both canonical and mirror-reversed trials[4] based on existing literature (e.g., Zhao, Della Sala, Gherri, 2019). The crucial question was whether M. X. would show the correlate of spatial transformation process during the letter rotation task, that is the RRN component, even though he is unable to summon a visual representation of the stimulus

[4] Although the RRN component is elicited and modulated by rotation angles during the MR processes of both canonical and mirror-reversed letters, distinct mechanisms are assumed to underlie the MR processes of these types of letters (Núñez-Peña et al, 2009; Quan et al., 2017). For instance, systematic differences between these conditions in terms of the RRN amplitude and time course have been well documented in the literature (Bajric, Rosler, Heil & Hennighaugen, 1999; Murray, 1997; Núñez-Peña et al, 2009). Some researchers have suggested the presence of an additional "flip-over" process during the MR of mirror-reversed stimuli as compared to canonical ones (e.g. Núñez-Peña et al, 2009). Thus, canonical and mirror-reversed letters not only differ with respect to their familiarity but also with respect to the cognitive load of the spatial transformation processes that participants have to engage to solve the MR task. It is therefore possible that M. X. will show a different pattern of results for the rotation of canonical and mirror-reversed stimuli.

in his mind's eye. If M. X. can complete the letter rotation task without showing typical RTs and RRN amplitudes increments associated with increasing rotation angles, this would provide converging evidence that individuals with aphantasia are unable to engage spatial transformation processes during MR tasks (c.f. Zeman et al., 2010). On the other hand, if he can complete the letter rotation task showing the typical RTs and RRN increments associated with the increasing rotation angles, this would suggest that individuals with aphantasia still retain the ability to engage the spatial transformation processes of MR, at least under specific circumstances (i.e., when stimuli are relatively easy to represent).

Because the present study was carried out several years after the original assessment of M. X.'s object imagery and mental rotation abilities (Zeman et al., 2010), it was relevant to assess whether the specific deficits originally highlighted in 2010 were still present or whether some form of recovery had taken place over the years. To this aim M. X. together with a group of sex-, age- and IQ-matched controls were tested on the MRT with arm-like cubes objects originally discussed in Zeman et al.'s report (2010). Like previous observations (Zeman et al., 2010), M. X. showed an accuracy rate comparable to that of controls but a non-linear pattern of RTs as a function of the increasing rotation angle (for more details, see results in Appendix I & II). In addition, M. X. confirmed he was still unable to create a mental image of the visual stimuli in his mind. Thus, it appeared that no form of spontaneous recovery had taken place.

Methods

Participants

M. X., 71-year-old at the time of testing, and twelve controls (different from the thirteen controls reported in Appendix I) were recruited for the present letter rotation task. One control was excluded from the analyses due to his low accuracy in both conditions. The control participants were matched for age (mean = 70.8, range 65-76 years old), handedness (righthanded), gender (male), IQ and education (13-15 years) with M. X. We administered three standard tests: (1) IQ: Wechsler adult intelligence scale-III (Wechsler, 1997); (2) subjective vividness of visual imagery: vividness of visual imagery (Marks, 1995); (3) visuospatial working memory: Corsi block task (Corsi, 1972; Kessels, van den Berg, Ruis & Brands, 2008).

All participants had no history of neurological or psychiatric disorders, had normal or corrected normal vision and all gave informed consent to participate in the study.

Stimuli and procedure.

On each trial, one of the uppercase letters F, L, P and R was presented in its canonical or mirror-reversed version rotated either 0°, 30°, 60°, 90°, 120° or 150° clockwise or counter-clockwise from its vertical upright position. The letters had a height of 3 cm, subtending 2.26° of visual angle. As shown in Fig.1, each trial began with the presentation with the presentation of a white fixation cross (1 cm *1 cm) in the centre of a black background. One hundred millisecond later, a white letter stimulus was presented in the central of the screen for 500 ms. After stimulus offset, the central fixation cross appeared and remained on the screen for a variable interval randomly selected between 1800- 2100 ms, during which responses were recorded.

Letters were presented in blocks of 96 trials each. Each combination of letter (F, L, P, R), stimulus parity (canonical vs. mirror-reversed), rotation angle (0°, 30°, 60°, 90°, 120° or 150°) and orientation of the rotation (clockwise vs. counter-clockwise) occurred ten times resulting in 960 experimental trials.

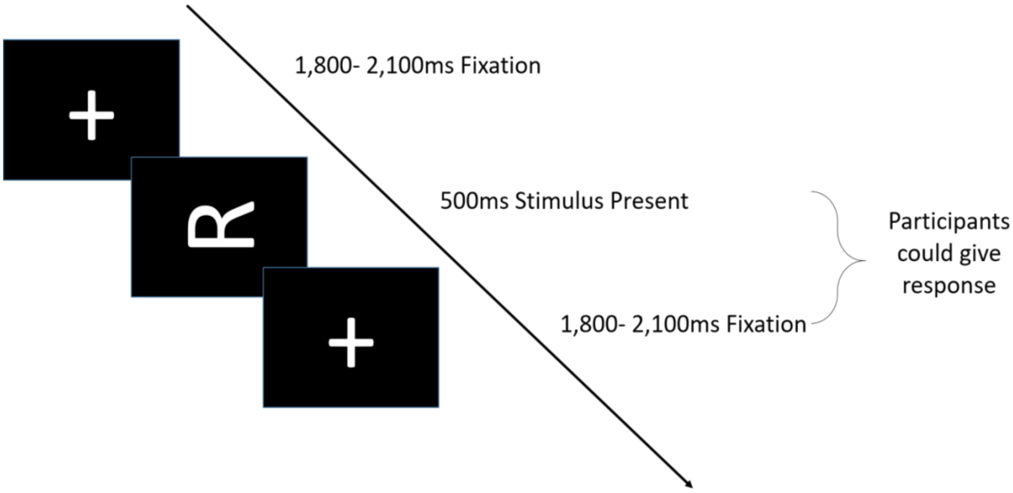

Fig.1: The experimental design in the present study.

Participants were instructed to respond as fast and as accurately as possible to the orientation of the letter (canonical vs. mirror-reversed letter), by pressing one of two vertically arranged buttons. During the task, participants were instructed to keep their eyes on the fixation cross on the screen and their index fingers on the response buttons. The top and bottom keys were associated with responses to canonical and mirror-reversed letters, respectively. While the stimulus to response mapping remained constant throughout the study, to avoid potential confounds associated with lateralised motor potentials, participants were asked to swap the responding fingers at the beginning of each block (left hand on top key and right on bottom or vice-versa). Before the experiment begun, participants completed a training block of 48 trials to familiarize themselves with this MRT. In this block of trials, the letters “G” and “J” were used as stimuli which were not included in the set of experimental stimuli.

EEG Recoding and pre-processing

EEG was acquired continuously from 64 active electrodes (BioSemi Active Two system) at a sampling rate of 512 Hz. Two electrodes positioned on the left and right ear lobes served as references. The horizontal EOG (hEOG) and vertical EOG (vEOG) were measured from four additional electrodes placed on the outer canthi of the eyes and the sub- and supra-orbital ridges of the right eye, respectively, and were calculated offline as the difference between these electrodes. The EEG signal was digitally re-referenced to the average of the left and right reference electrodes. 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 of 850 ms, from 100 ms before to 750 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 ±70 μV at any scalp electrodes) throughout the epoch were excluded from the analysis. Participants' averages were computed on correct trials for each combination of stimulus parity (canonical, mirror-reversed) and rotation angle (0°, 30°, 60°, 90°, 120°, 150°). Data from trials with different letters and different directions of rotation (clockwise, counter-clockwise) was collapsed across.

Data analyses

For each rotation angle, trials with clockwise and counter-clockwise rotations were combined for both the behavioural and ERP data analysis. To test whether M. X. shows a deficit in this letter rotation task, the accuracy rates collapsed across all rotation angles (0°, 30°, 60°, 90°, 120° and 150°) were first analysed for the canonical and mirror-reversed letters separately. The procedure developed by Crawford and Garthwaite (2002; see also Crawford & Howell, 1998) was implemented[5] to compare the accuracy rates between M. X. and the control group. In contrast to the use of z-scores, the current method treats the control sample statistics as statistics rather than as parameters and compares the single subject's score to the control group's score by using a non-central *t* distribution.

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[5] The program singlism.exe (available in http://homepages.abdn.ac.uk/j.crawford/pages/dept/SingleCaseMethodology.htm) was applied.

Following the same procedure used for the accuracy rates (Cawford & Garthwaite, 2002; Craw & Howell, 1998), a first comparison was conducted on RTs for letters in the upright position (0°) between M. X. and the control group for the canonical and mirror-reversed letters separately. Then, we analysed RTs differences between M. X. and controls for rotated letters (30°, 60°, 90°, 120° and 150°) which was the main contrast of interest. RTs for rotated letters were corrected in order to control for the potential influence of the inter-participant difference in baseline performance (0°) (c.f. Logie et al., 2011). That is, for each participant each rotation angle (30°, 60°, 90°, 120° and 150°) mean RTs was subtracted from that measured on no rotation trials (0°). The Crawford and Garthwaite's procedure (2002) was then applied on these corrected RTs for canonical and mirror-reversed trials separately to test whether M. X. performed differentially across all rotation angles as compared to the controls.

Additional analyses were conducted to further characterize the performance associated with different rotation angles in M. X. and the control group. First, the Pearson correlation coefficient was computed for individual participants separately for trials with canonical and mirror-reversed letters to test whether the typical RTs increment with rotation angles is present in M. X. and the control group[6]. The subsequent analysis with intra-individual measures of association (IIMAs; Crawford, Garthwaite, Howell & Venneri, 2003) was carried out[7] to compare the correlation coefficient between M. X. and the control group for each stimulus type. According to this method (Crawford et al., 2003), Fisher's transformation is applied to the correlation for individual participant as Pearson's *r* is not normally distributed. The

[6] A linear regression line could be fitted in controls' RTs in both canonical (all *p*-values ≤ .047) and mirror-reversed conditions (all *p*-values ≤ .043). M. X.'s RTs showed a linear trend in both the canonical ($p = .009$) and mirror-reversed conditions ($p = .043$). Therefore, the estimated slopes measured were computed by the linear trend analysis in each condition for further slope analyses. However, the analyses were rejected for both canonical and mirror-reversed letters as the error of at least one control was significantly smaller or larger than the other controls' error variances.

[7] The program iima.exe was used (available in http://homepages.abdn.ac.uk/j.crawford/pages/dept/SingleCaseMethodology.htm).

transformed correlation of M. X. was then compared with the mean and standard deviation of the transformed correlation in the control group using the *t*-distribution.

Mean amplitude values for the ERP analyses were quantified over central-parietal electrodes (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4) as selected in Quan et al. (2017) within a predefined measurement windows 350 – 650 ms post-stimulus for each participant, each stimulus type (canonical vs mirror-reveresed) and each rotation angle (0°, 30°, 60°, 90°, 120° and 150°). Methods of statistical analysis for ERP data were consistent with methods for behavioural data. First, the ERP amplitudes for letters in the upright position (0°; baseline) were compared between M. X. and his controls in the canonical and mirror-reversed conditions separately by applying Crawford and Garthwaite' procedure (2002; Craw & Howell, 1998). Then, RRN amplitudes were calculated by subtracting ERPs elicited by letters at 30°, 60°, 90°, 120° and 150° rotation angles from those elicited by upright letters (0°) to remove their baseline performance and the potential influence of inter-participant differences. The Crawford and Garthwaite's procedure (2002; Craw & Howell, 1998) was applied on the resulting RRN amplitudes collapsed across all rotation angles (30°-0°, 60°-0°, 90°-0°, 120°-0° and 150°-0°) separately for canonical and mirror-reversed trials to test whether M. X. performed differently from controls on rotated letters.

In addition, to further characterize the MR processing and to test whether the typical MR pattern can be observed in each experimental condition, the correlation coefficient between RRN amplitudes and rotation angles was calculated for M. X. and individual control participants separately in the canonical and mirror-reversed conditions. The IIMAs (Crawford et al., 2003) was then conducted to compare the corrected correlation coefficient (after Fishers' transformation) between M. X. and the control group[8].

Results

The demographic variables for M. X. and for the eleven controls are summarised in Table 1. M. X. was well matched with control participants on general intelligence (full scale IQ 136 in M. X. vs. 139 in the control group). In the VVIQ test (Marks, 1995), M. X. showed significant lower scores than the controls.

Table 1 Demographic variables for M. X. and matched controls.

	M. X.	Control mean	Control SD
Age	71	70.8	3.0
WAIS-III	136	137.8	5.9
VVIQ-2 (/160)	32^{***}	138.7	11.3
Corsi blocks	4	4.9	0.5

Behavioural data

The analysis of accuracy rates showed that M. X. (canonical = 96.3%; mirror-reversed = 94.2%) performed as well as his controls (canonical= 95.5% ± 3.1; mirror-reversed = 93.7% ± 3.7) during the MR of canonical (t (10) =0.24, p = 0.41) and mirror-reversed letters (t (10) =0.13, p = 0.90). The estimated percentage of normal population performing worse than M. X. is 38.87% for canonical and 32.20% for mirror-reversed letters.

The RT analysis revealed no difference between M. X. and the control group on trials with upright letters (baseline condition) for both canonical (M. X. =541.37ms, controls = 699.17ms, SE = 158.27; t (10) =-.96, p = .18) and mirror-reversed letters (M. X. =780.36ms, controls

[8] ERPs for M. X. could be described as a linear trend in the canonical condition (p = .007) but not in mirrored letter processing (p = .478). Therefore, the slope of ERP amplitudes could not be obtained for further analysis.

=784.91ms, SE = 147.09; *t* (10) =-.03, *p* = .49). For trials with rotated letters, M. X. and controls did not differ on canonical letter trials (corrected RTs: M. X. =135.59ms, Controls = 138.43ms, SE = 68.13), *t* (10) =-0.04, *p* = .484. However, for mirror-reversed letters M. X. (corrected RTs = 94.06ms) performed faster than his controls (corrected RTs = 197.07ms, SE = 55.76), *t* (10) =-1.77, p = .054), see Fig.2, right panel.

On canonical letter trials (Fig.2, left panel) both M. X. and controls showed a positive association between corrected RTs and rotation angles (M.X: *r* = .96, *p* = .009; control group: *r* = .77, p < .001). Further IIMAs analyses on the transformed correlation coefficients (corrected r': M. X. =1.97; controls =1.83 ± 0.28) revealed that there was no difference between M. X. and controls on canonical letter trials, *t* (10) =0.49, *p* = 0.32. The estimated percentage of normal population falling below M. X.'s coefficient is 44.63%.

On mirror-reversed letter trials (Fig.2, right panel), the positive association between corrected RTs and rotation angle was evident for both M. X. (*r* = .96, *p* = .009) and controls (*r* = .78, *p* < .001). The IIMAs revealed that the transformed correlation coefficient between RTs and rotation angles measured in M. X. did not statistically differ from that of controls (corrected *r*': M. X. =1.42; controls = 1.72 ± 0.35; *t* (10) =-0.82, *p* = .22). The estimated percentage of normal population showing a smaller –association between RTs and rotation angle as compared to M.X is 6.22%.

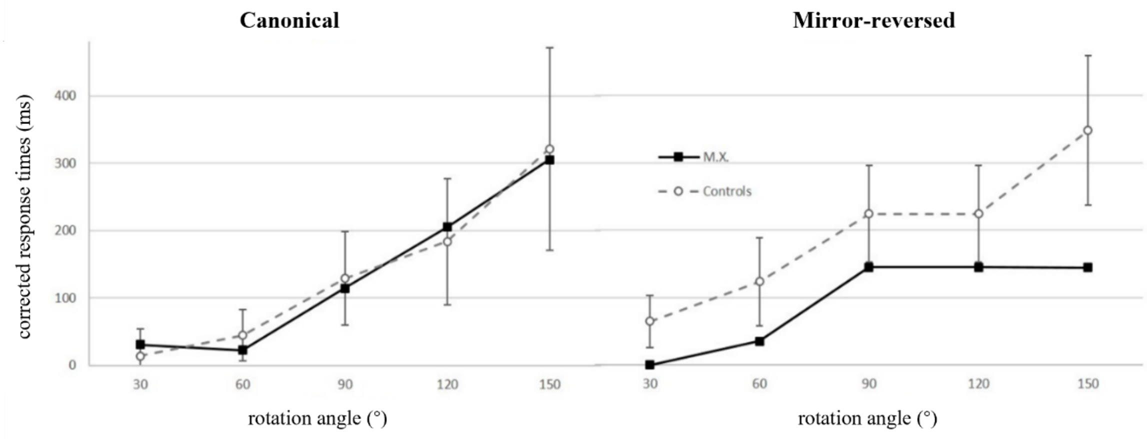

Figure 2. Mean corrected response times for canonical (left) and mirror-reversed (right) rotated letters in M. X. (solid line) and the control group (dashed lines). Corrected RTs were calculated for each participant by subtracting the mean RTs obtained on each of the different rotation angle trials (30°, 60°, 90°, 120° and 150°) from the mean RTs on no rotation (0°) trials. Error bars represent 95% confidence interval.

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Event-related potentials

For trials with letters in the upright position (0°; baseline condition), larger ERP amplitudes were observed for M. X. (canonical =9.27µV; mirror-reversed = 12.06µV) as compared to his controls (canonical = 3.20µV ±± ± 1.6; mirror-reversed = 3.88µV ±± ± 2.4) on canonical (t (10) =3.72, p = 0.002) as well as mirror-reversed letters trials (t (10) =3.23, p = 0.005).

For trials with rotated letters, there was no difference in the RRN amplitudes (the ERP difference waves collapsed across all rotated letters) between M. X. and controls for both canonical (t (10) = -.01, p = .50) and mirror-reversed letters (t (10) = 1.40, p = .09) after correcting for intra-participant baseline.

The RRN amplitudes across rotation angles were further characterized for M. X. and his controls for trials with canonical and mirror-reversed letters separately by examining the correlation coefficient between rotation angles and RRN amplitudes. During the MR of canonical letter, there was a significant correlation between RRN amplitudes and rotation angles in both M. X. (r = -.97, p = .007) and controls (r = -.47, p < .001). For both M. X. and controls (Fig.3, left panel), RRN amplitudes became more negative with increasing rotation angles. IIMAs analyses confirmed that the coefficient measured in M. X. on canonical letter trials (r'=-2.03) was not statistically different from that observed in the control group (r' =-1.09 ± 0.73), t (10) = 1.24, p = 0.12. The estimated percentage of normal population falling below M. X.' rotation coefficient in the canonical condition is 67.75%.

On mirror-reversed letter trials (Fig.3, right panel), the control group showed a significant correlation between RRN amplitudes and rotation angles (r = -.47, p < .001), indicating that the RRN became more negative with increasing rotation angles. However, M. X. showed no such correlation (r = .42, p = .48). The IIMAs carried out on the transformed correlation coefficient between RRN amplitudes and rotation angles revealed a significant difference between M. X. (r' =.45) and controls (r' =-.83 ±± ± 0.61) on mirror-reversed letter trials, t (10) =-2.01, p = 0.036. The estimated chance for the normal population to show an association between the RRN and the rotation angle lower than M. X. on mirror-reversed letter trials was only 0.08%.

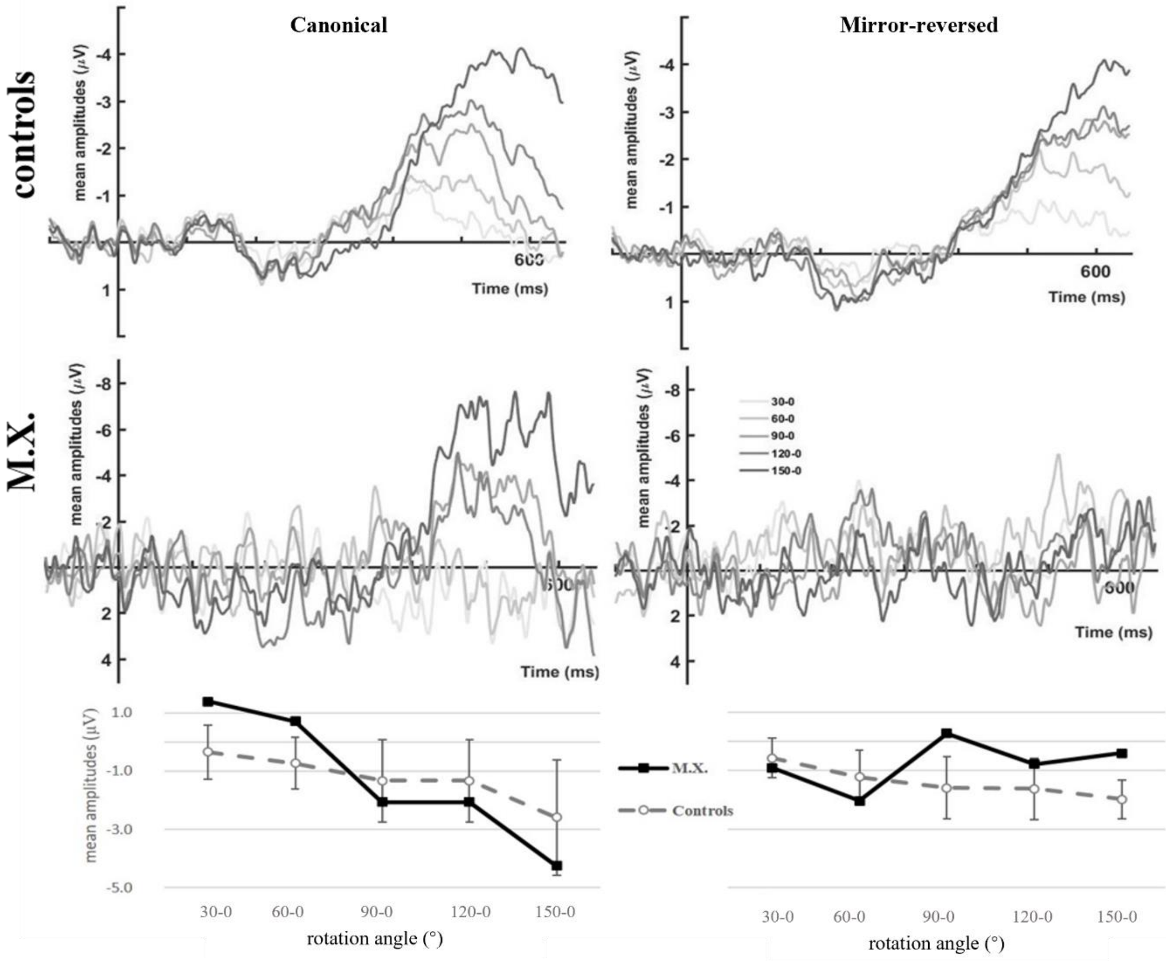

Figure 3. The top and middle panels show the RRN components calculated as the difference waveforms between ERPs elicited by rotated letters (30°, 60°, 90°, 120°, 150°) from those elicited by upright letters (0°) over pooled central-parietal sites (Cpz, Cp1/2, Cp3/4, Pz, P1/2, P3/4). These subtraction waveforms

are shown separately for canonical (left panels) and mirror-reversed letters (right panels) and for the control group (top panels) and M. X. (middle panels). The corresponding mean amplitude values (in microvolts) calculated in the 350-650ms time window are shown in the bottom panels separately for M. X. (black solid line) and his matched controls (grey dashed line). Error bars show 95% confidence intervals.

Discussion

M. X. is an individual affected by acquired aphantasia. He reportedly lost the ability to experience voluntary visual imagery and to create conscious depictive mental representations. His imagery deficit was first described by Zeman and colleagues in 2010. Several years later, at the time of testing for the present study, M. X. was still complaining about his aphantasic deficit. When we assessed his blind imagination, he showed a significantly lower VVIQ score as compared to his age-, gender-, education- and IQ-matched control participants. In addition, when tested again on the arm-like cube task initially used by Zeman and colleagues (2010), M. X. still showed a non-linear pattern of RTs as a function of the increasing rotation angles compared to controls. These observations together with his self-reported inability to visualize objects in his mind's eye suggest that there had not been spontaneous recovery of his voluntary imagery abilities during the intervening years.

The present ERP study sought to clarify whether M. X. retained the ability to engage the spatial transformation process of MR during a MRT despite his inability to experience visual imagery. To this aim, M. X. and his controls were asked to complete a letter rotation task while behavioural and electrophysiological responses were recorded. We were specifically interested in the RRN component of ERPs which is considered a direct electrophysiological correlate of MR (Heil 2002). In line with existing literature, ERPs and behavioural analyses were carried out separately for canonical and mirror-reversed letter trials because the processing and rotation of canonical letter may differ from that of mirror-reversed letters (e.g., Núñez-Peña & Aznar-Casanova, 2009; Martinaud et al., 2016).

On canonical letter trials, no difference was observed between M. X. and controls with respect to the behavioural or the ERPs data. Specifically, M. X. was as accurate as controls and showed the typical increasing RTs pattern as a function of the increasing rotation angles also observed in the control group. Furthermore, M. X. showed the presence of a reliable RRN component during the MR of canonical letters. The amplitude of the RRN observed for M. X. was modulated by rotation angle with increasing negativities as a function of the increasing letter rotation angles, similarly to what observed in controls and described in the ERP literature (e.g. Heil, 2002). This finding suggests that M. X. was able to execute in his mind the spatial transformation process of canonical letters to complete the MRT despite his self-reported inability to create depictive mental representations of objects.

The presence of the RRN component and its amplitude modulations by rotation angle suggests that at least for canonical letters, M. X. has retained the ability to spatially transform the stimuli in his mind. Christophel and his colleagues (2015) using a combination of functional MRI and multivariate decoding were able to identify the distinct brain areas involved in the generation and manipulation of mental images in a MRT. The initial image retrieval from memory was associated with an active pattern in early visual areas whereas the transformation of these contents during the MR processes was accompanied by brain activity in the posterior parietal cortex (Christophel et al., 2015). In line with this dissociation, it is possible that the spatial transformation process of MR which is assumed to occur in parietal areas is preserved in M. X. as indicated by the presence of the RRN component.

These findings also suggest that M. X. was able to create a mental representation of the letter whose format was compatible with (supported) the spatial transformation processes of MR indexed by the RRN. Depictive mental images have been considered necessary for MR processes (Paivio, 1971; Kosslyn et al., 2006). The inability of M. X. to engage the posterior brain network responsible for face imagery (Zeman et al., 2010), suggests that he is unable to recruit visual imagery brain areas. Recently, Pearson and Kosslyn' (2015) have argued that multiple formats of representation can be generated for the same objects, such as symbolic, language-like (i.e. inner speech, verbal reasoning or mental operation in rhythm; Li, Luo & Tian, 2020), descriptive formats (i.e. propositional/non-depictive; Pylyshyn, 1981, 2003) as well as a depictive (e.g., Kosslyn, Thompson, & Ganis, 2006; Paivio, 1971). Furthermore, different brain areas are known to be recruited during the activation of different mental representations formats, such as visual cortices for depictive representation (Cui et al, 2007; Fulford et al., 2018), and the inferior frontal gyrus for sematic or symbolic representations (IFG; Montefinese, 2019; Wang et al., 2018). Given M. X.'s inability to activate brain areas responsible for visual imagery and conscious depictive representations (Zeman et al., 2010), it is possible that he defaulted to a different type of mental representation and that he was able to apply the spatial transformation processes of MR to a non-depictive mental representation of the letter.

On mirror-reversed letters trials, M. X. showed a high accuracy rate (>90%) demonstrating that he was able to complete the MRT successfully. However, he performed differently from controls as indicated by both behavioural and ERPs measures. Although both M. X. and controls showed the typical linear association between RTs and rotation angles, M. X. responded faster than controls across rotation angles. ERP results showed no evidence for the presence of the RRN in M. X., while the expected RRN modulation by rotation angle was present in the control group. Together, these findings suggest that was able to complete successfully the MRT without engaging the spatial transformation processes of MR.

Although it is likely that the spatial transformation processes of MR indexed by the RRN are the default cognitive process used in MRTs, it is not the only process that allows participants to complete the task. The choice of different cognitive/analytical strategies adopted in a MRT is flexible and can be influenced by several factors. For example, some of these factors are related to individual differences amongst participants such as their gender (Heil & Jansen-Osmann, 2008), age (Zhao, Gherri & Della Sala, 2020) and mental imagery abilities (Zhao & Della Sala, 2018; Zhao, Della Sala, & Gherri, 2019). Other factors are specifically related to the task such as the familiarity or the complexity of the stimuli (Zhao, Zhu & Della Sala, 2019). The fact that M. X. was able to complete the MRT with mirror-reversed letters in the absence of MR processes provides supporting evidence for the argument that the spatial transformation process of MR is not necessary to successfully complete a MRTs (e.g., Cooper & Shepard, 1973; Marmor & Zaback, 1976; Pearson & Kosslyn, 2015).

Behavioural results for mirror-reversed stimuli show comparable performance for M. X. and controls with similar accuracy levels and the linear increase observed in RTs as a function of rotation angles. These results do not offer any clear indication about the strategy he may have used to solve the MR of mirror-reversed stimuli. Because the RRN is considered the electrophysiological correlate of the spatial transformation process of MR whereby the mental representation of the stimulus is holistically rotated in the participants' minds (Heil, & Rolk, 2002), it would be tempting to conclude that its absence indicates M. X. had adopted an analytic or piecemeal rotation process instead. However, the RRN component is calculated by averaging ERP waveforms over many trials in which the same stimulus is presented. Variations across trials in the onset time of the spatial transformation process of MR or variations of the strategy adopted could have resulted in the overall absence of the RRN component. For these reasons, while it is not possible to draw firm conclusions about the specific alternative strategy that M. X. adopted to rotate mirror-reversed letters, it is possible to rule out that he adopted systematically the spatial transformation processes indexed by the RRN.

The finding that the spatial transformation processes of MR as indexed by the RRN were observed only for canonical letters but not for mirror-reserved letters suggest that the familiarity of the stimuli may have influenced the type of mental representation that M. X. was able to activate and, consequently, the type of mental transformation process applied to it. Canonical letters are highly familiar stimuli that are over-learned throughout life. It is therefore conceivable that the mental representations of canonical letters can be readily accessed through memory. A very close correspondence between the mental representations underlying visual working memory and visual imagery has been suggested based on both cognitive (Borst, Ganis, Thompson, & Kosslyn, 2012) and imaging evidence (Albers et al., 2013, Slotnick et al., 2012). It is therefore possible, that canonical letters may have activated different mental representations compared to those of mirror-reversed letters simply due to the possibility of accessing the canonical representations through different memory channels.

Results of the present study demonstrated that M. X. can, under specific circumstances, engage the spatial transformation process of MR despite his reported inability to generate object imagery. This pattern of results offers some new insight into the mechanisms responsible for aphantasia. Recent evidence has shown that it is possible to engage involuntary imagery in MRTs (Cushing, Gazzaley, & Morsella, 2019). Accordingly, one may ask whether M. X.'s deficit concerns the conscious access of the content of visual imagery rather than its voluntary generation. In other words, one may ask whether aphantasia is caused by an impaired metacognition of visual imagery. If M. X.'s deficit was simply related to the inability to consciously access the content of visual imagery, similar spatial transformation processes, i.e., similar RRN components, should have been observed regardless of the type of stimulus involved in the MRT. By contrast, results of the present study showed a different pattern of spatial transformation processes of MR for canonical and mirror-reversed letters, arguing against this possibility.

In sum, the current finding that M. X., a case of aphantasia, can successfully complete a letter MRT with both canonical and mirror-reversed letters provides evidence that MRTs can be completed in the absence of conscious depictive representations. Importantly, the presence of the RRN component in M. X. and the fact that its amplitude linearly increased with rotation angles during canonical letter rotation suggest that M. X. was able to adopt the spatial transformation process of MR. Together these findings reveal that individuals with aphantasia can show spared spatial transformation ability (cognitive manipulation of a mental representation) in the absence of voluntary object imagery.

Appendix I:

Behavioural Results for MRTs with typical arm-like cubes objects

Accuracy rates

The accuracy rates were analysed collapsing across all rotation angles (0°, 40°, 80°, 120°, and 160°) and two stimulus parities (identical vs. mirror-reversed). M. X. (mean =61.26%) showed no deficit in completing the typical MRT with arm-like cube objects as compared to his controls (M = 66.05%, SD =8.18%, t = -.56, one-tail p = .29). The estimated percentage of normal population performing worse than M.X is 29.14%.

Response times

Like the method reported in the main text, for each rotation angle, trials with clockwise and counter-clockwise rotations as well as different stimulus parities (identical and mirror-reversed) were combined. RTs for rotated stimuli were corrected to control the potential influence of the inter-participant difference in baseline performance (0°). To test whether M. X. performed differentially as on all rotation angles as compared to his controls, Crawford and Garthwaite's procedure (2002) was carried out first on RTs for stimuli in the upright position (0°) and the corrected RTs for rotated angles separately. Intra-individual measures of association (IIMAs; Crawford, Garthwaite, Howell & Venneri, 2003) was then applied on the correlation coefficient between M. X. and his controls to further investigate the existence of the typical RTs increment with rotation angles. Fisher's transformation was carried out if Peason's r is not normally distributed.

The RTs analysis revealed no difference between M. X. and his controls on stimuli on upright position (0°; M. X. = 4569.9ms, controls =4750.8ms, SD =2534.7ms, t = -.069, p =.946) as well as the rotated angles (M. X.'s corrected RTs = 1797.2ms, controls' corrected RTs =

696.3ms, SD = 608.4ms, t =1.311, p = .214). As shown in Appendix II, the positive association between RTs and angles was evident for the control group (dashed line; r =.57, p = .012) but not for M. X. (solid line; r = .20, p =.077). The IIMAs further revealed that the transformed correlation coefficient between RTs and rotation angles measured in M. X. (correctd r'= .22) was significantly lower than his controls (correct r' =.44, corrected SD =.062, t (12) = -3.40, p =.003). The estimated percentage of normal population fallowing below M. X.'s coefficient is 0.26%.

Appendix II:

Figures on Response times (RTs) in MRTs with typical arm-like cubes

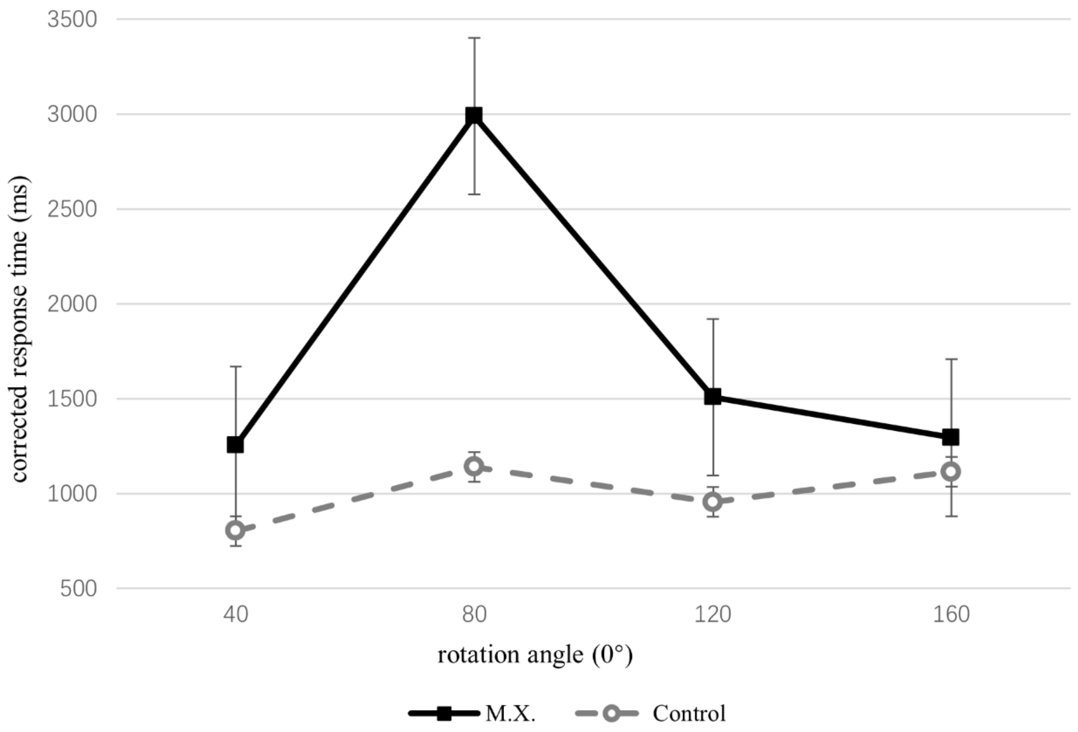

Figure: Response times on each rotation angles in M. X. (solid line) and his controls (dashed line) in a MRT with the typical arm-like cube objects as visual stimuli.

Declarations

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Conflicts of interests

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval

All study procedures were approved by the Psychology Committee, University of Edinburgh.

Consent to participate

Informed consent was obtained from all individual participants included in the study.

Consent to publish

The participant has consented to the submission of the case report to the journal.

Availability of data and materials

The raw data and the visual stimuli of the present experiment is available to public and could be obtained by request from the first author.

Code availability

For data analysis, we used the program iima.exe (available in http://homepages.abdn.ac.uk/j.crawford/pages/dept/SingleCaseMethodology.html). There is no specific data analysis script used and available for the present experiment.

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