CORTEX XXX (XXXX) XXX

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research Report

Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery

Zoë Pounder [a,*], Jane Jacob [b], Samuel Evans [a], Catherine Loveday [a], Alison F. Eardley [a] and Juha Silvanto [c]

[a] School of Social Sciences, University of Westminster, London, UK
[b] Department of Psychology and Behavioural Sciences, Louisiana Tech University, USA
[c] School of Psychology, University of Surrey, Surrey, UK

ARTICLE INFO

Article history:
Received 20 May 2021
Reviewed 24 June 2021
Revised 16 September 2021
Accepted 17 December 2021
Action editor Paolo Bartolomeo
Published online xxx

Keywords:
Aphantasia
Visual imagery
Spatial imagery
Neuropsychology

ABSTRACT

Aphantasia describes the experience of individuals who self-report a lack of voluntary visual imagery. It is not yet known whether individuals with aphantasia show deficits in cognitive and neuropsychological tasks thought to relate to aspects of visual imagery, including Spatial Span, One Touch Stocking of Cambridge, Pattern Recognition Memory, Verbal Recognition Memory and Mental Rotation. Twenty individuals with congenital aphantasia (VVIQ < 25) were identified and matched on measures of age and IQ to twenty individuals with typical imagery (VVIQ > 35). A group difference was found in the One Touch Stocking of Cambridge task for response time, but not accuracy, when the number of imagined moves that participants had to hold in their heads to complete the task increased. Similarly, a group difference in response time was apparent in the mental rotation task, but only in the subgroup of aphantasic participants who reported a severe deficit in visual imagery (VVIQ score of 16). These results suggest that the cognitive profile of people without imagery does not greatly differ from those with typical imagery when examined by group. In addition, the severity of aphantasia (and VVIQ criterion) may be an important factor to consider when investigating differences in imagery experience. Overall, this study raises questions about whether or not aphantasia represents a difference in cognitive function or in conscious experience.

* *Corresponding author*. Department of Psychology, University of Westminster, London, UK.
E-mail address: z.pounder@westminster.ac.uk (Z. Pounder).

https://doi.org/10.1016/j.cortex.2021.12.010
0010-9452/

1. Introduction

Most people self-report that they experience visual mental imagery, in other words, they have the ability to create an image in their mind's eye in the absence of direct perceptual information (Galton, 1880; McKelvie & Demers, 1979). However, a subset of the population, those with aphantasia, self-report an absence of visual imagery, despite having no obvious neurological impairment (Faw, 2009; Keogh & Pearson, 2018; Zeman, Dewar, & Della-Sala, 2015). Aphantasia can be acquired following neurological injury (e.g., Bartolomeo, 2002; Farah, 1984; Zeman et al., 2010) or present from birth (e.g., Keogh, Pearson & Zeman, 2021; Zeman et al., 2015).

Up to now, much exploration of aphantasia has been based on subjective report, although there is some evidence to show that objective differences are apparent between people with aphantasia compared to people with typical imagery. For example, individuals with aphantasia reported less sensory sensitivity in self-reports and less sensitivity in a visual pattern glare task (Dance et al., 2021b). Similarly, individuals with aphantasia were less susceptible to flicker induced pseudo-hallucinations (Konigsmark, Bergmann, & Reeder, 2021). Preliminary evidence suggests that individuals with aphantasia may have reduced visual attention (Keogh & Pearson, 2021; Monzel, Keidel, & Reuter, 2021) and are more likely to score higher for autism traits than typical imagers (Dance et al., 2021). Specifically in terms of imagery tasks, the lack of visual imagery reported by individuals with aphantasia affects their performance in tasks such as binocular rivalry (Keogh & Pearson, 2018), visual memory performance assessed through drawing (Bainbridge, Pounder, Eardley, & Baker, 2020) and in reduced physiological response when reading frightening fictious scenarios (Wicken, Keogh, & Pearson, 2021). What is not yet clear is what underpins the apparent differences in imagery experience.

A straight-forward question is whether aphantasia may reflect other underlying cognitive deficits that manifest as differences in performance within neuropsychological tasks. Reported in case studies, potential deficits in aphantasic individuals have already been noted in relation to working memory and/or executive function. Jacobs, Schwarzkopf & Silvanto (2017) noted in a case study of the congenital aphantasic participant *AI*, that she performed less accurately within a visuo-spatial working memory task at the highest level of difficulty relative to controls. However, no differences in accuracy were apparent in a matched imagery version of the task compared to control participants. Although they were discussing acquired aphantasia, it is worth noting that Zeman et al. (2010) reported in their case study that Patient *MX* displayed longer reaction times but equivalent accuracy to neurotypical controls in a Mental Rotation Task (MRT), a classic visuo-spatial imagery task thought to involve working memory function (e.g., Shepard & Metzler, 1971). The authors explained this in terms of *MX* adopting a different strategy in the task (Zeman et al., 2010). *MX*'s performance was nevertheless normal on a range of executive function tasks (Zeman et al., 2010). Within larger samples, individuals with aphantasia perform as accurately to individuals with typical imagery in range of clinical and non-clinical visual working memory paradigms (Keogh, Wicken & Pearson, 2021). Similarly, individuals with aphantasia perform as accurately as typical imagers in a range of clinical memory tasks (e.g., task assessing anterograde memory, Milton et al., 2021) and do not show visual recognition memory deficits (Bainbridge et al., 2020; Milton et al., 2021). In the study by Milton et al. (2021), the authors also showed that participants with aphantasia were as accurate as typical imagers on a Manikins test involving the mental rotation of a human avatar (Milton et al., 2021), however, response time was not measured. Broadly, the studies which have adopted larger sample sizes to explore objective differences between participant groups have only assessed performance by comparing accuracy (e.g., Keogh et al., 2021; Milton et al., 2021) when measures such as response time may be more informative with regards to differences in strategies used within tasks (Zeman et al., 2010).

Potential deficits have also been noted in relation to episodic memory, such that individuals with aphantasia reported lower levels of episodic memory compared to typical imagers (Dawes, Keogh, Andrillion, & Pearson, 2020). Recent work has also reported subjective impairments in autobiographical memory in aphantasic individuals relative to typical imagery controls (Dawes, Keogh, Andrillon, & Pearson, 2020; Milton et al., 2021). Although both working memory and episodic memory have been previously reported as being potential areas of weakness or impairment in aphantasia (Dawes et al., 2020; Milton et al., 2021; Jacobs et al., 2017), studies investigating this objectively using larger sample sizes are limited.

To address the gap in knowledge around core cognitive deficits, we selected four tests from the Cambridge Neuropsychological Test Automated Battery (CANTAB). The tasks were: Verbal Recognition Memory (VRM), Pattern Recognition Memory (PRM), Spatial Span (SSP) and One Touch Stocking of Cambridge (OTS). The MRT, a classic visuo-spatial imagery task and measure of spatial ability involving object rotation (Shepard & Metzler, 1971; Xue et al., 2017), was also included in the battery. These tasks tap into two domains thought to be essential to the imagery process: declarative memory (VRM and PRM) and visuo-spatial working memory (SSP, OTS and MRT). These broadly map on to hippocampal and prefrontal brain regions respectively, although these regions are relevant to a range of other non-imagery tasks.

Pattern recognition (PRM) was selected in order to compare visual memory performance, with verbal memory (VRM). If impaired on both, then a general declarative memory (i.e., conscious hippocampal-dependent memory (Squire, 1992)) impairment may be assumed. If impaired only on visual memory, then the deficit would be specific to visual declarative memory. However, if performance is within the normal range for both of these tasks then this provides initial evidence that they are not clinically impaired on declarative memory.

Both SSP and OTS are considered an assessment of visual working memory. The SSP is a visual sequencing working memory task, often used as a classic measure of visuo-spatial working memory capacity (Levaux et al., 2007). The strength of visual imagery correlates with visual working memory capacity (Keogh & Pearson, 2014). This suggests the stronger

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

one's visual imagery, the greater their visual working memory capacity. Patt et al. (2014) states that a key strategy for performance on the SSP is the generation of visual imagery by 'making shapes' from imaginary lines. In contrast, the OTS requires the maintenance and manipulation of increasing amounts of visuo-spatial information in working memory, a process suggested to engage visual imagery (Hodgson, Bajwa, Owen, & Kennard, 2000). If impairments are evident on the SSP then this suggests a fundamental impairment in holding a visual sequence in mind, which might also be expected to correspond to impairments in the OTS task given that both tasks require the maintenance of visuo-spatial information. However, if there is normal performance on the SSP but not on the OTS, then it follows that the impairment may be due to difficulties with manipulating the information rather than just maintaining the information in mind, which becomes more difficult with increasing number of items to manipulate. It is important to note that the OTS also has a planning and strategy element, which more directly reflects executive function and does not necessarily implicate the visuo-spatial system.

The MRT was chosen to supplement these visuo-spatial tasks as, like the OTS, it requires manipulation and is traditionally assumed to rely on visual imagery, but unlike the OTS it does not require any additional planning or memory component. As such, if a difference was found in the MRT and the OTS, this would suggest an impairment in the manipulation element, but if impairment was only found in the OTS, then it might suggest an impairment in planning and strategy. Nevertheless, it is important to note that whilst the SSP, the MRT, and the OTS are defined as visual working memory tasks, they have strong spatial components (Foster, Bsales, Jaffe, & Awh, 2017; McCants, Katus, & Eimer, 2019). Evidence from congenitally totally blind individuals suggests that working memory tasks traditionally considered to rely on visual processes, including the MRT, can be carried out without visual experience (e.g., Carpenter & Eisenberg, 1978; Kerr, 1983; Marmor & Zaback, 1976; Zimler & Keenan, 1983).

In summary, this study uses clinical tests to investigate declarative memory and visuo-spatial working memory in a group of individuals with aphantasia and typical imagery. Firstly, it examines declarative memory performance in people who self-report a lack of visual imagery, specifically assessing whether deficits are specific to the visual domain. Secondly, it assess whether deficits specifically emerge when the demands for holding and manipulating visuo-spatial information increase.

2. Materials and methods

The data reported here was part of a larger battery of tasks, that were carried out over two separate testing sessions of 2 h each, one week apart. There were two testing sessions. There was a fixed set of tasks within each of the two sessions. The order of the two sessions was counterbalanced across participants. A Latin square was used to permute the order of the tasks within each session. Both groups undertook the same sequence of tasks. Hence, within and between session order effects were accounted for and balanced across groups. At the beginning of each task, all participants were informed not to use hand or head gestures (or any part of their body) to aid calculation. This is because hand gestures have been shown to aid cognitive processing and improve performance within a range of complex visuospatial tasks (Alibali, Spencer, Knox, & Kita, 2011; Eielts et al., 2020). The protocol for the study was in accordance with the British Psychological Society guidelines and the ethical approval provided by the Psychology Department Ethics Committee of the University of Westminster, UK (ETH1617-0039). All data can be accessed on OSF (https://osf.io/erksc/). We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedures or analysis was preregistered prior to being undertaken.

2.1. *Participants*

Twenty (7 males, 13 females) individuals with congenital aphantasia were recruited from aphantasia-specific online forums, including "Aphantasia (Non-Imager/Mental Blindness) Awareness Group", "Aphantasia!" and Aphantasia discussion pages on Reddit. All aphantasic participants reported a life-long inability to generate visual imagery and no history of mental illness (confirmed via email correspondence and verbally during the first testing session). Control participants (those with typical visual imagery) were recruited from students and staff at the University of Westminster as well as recruited through social media (they also confirmed via email correspondence and verbally no history of mental illness). At present, there is no agreed cut-off score for defining groups based on typical and atypical self-reports of imagery (Zeman et al., 2015), congenital aphantasic participants (n = 20: 7 males, 13 females) were identified through the Vividness of Visual Imagery Questionnaire (VVIQ), defined by scores $\leq$25 (M = 16.65, SD = 1.95, range: 16–24). The maximum score provided on the VVIQ by aphantasic participants was 24, therefore no participants were excluded. Typical imagery control participants (n = 20: 8 males, 12 females) were identified by VVIQ scores $\geq$ 35 (M = 63.8, SD = 12.34, range: 36–80). These mean VVIQ scores for typical imagers are in line with the normative VVIQ scores of 'normal' imagery experience as identified in a meta-analysis (McKelvie, 1995). Individuals with congenital aphantasia did not differ from controls on age (aphantasic age: M = 40y0m, SD = 8.92; control age: M = 39y6m, SD = 11.61; t(38) = .28, p = .78, d = .04). They also did not differ on Weschler Adult Reading Test (WTAR; Wechsler, 2001), which can be used as a proxy measure for intelligence (Mathias, Bowden, & Barrett-Woodbridge, 2007) (aphantasic WTAR score: M = 43.35, SD = 3.01 or predicted Full-Scale IQ (FSIQ) equivalence: M = 108, SD = 3.21; control WTAR score: M = 42.30, SD = 4.12 or predicted FSIQ equivalence: M = 106.6, SD = 4.42, WTAR: t(38) = .92, p = .36, d = .29). All participants had normal or corrected-to-normal vision and no history of mental health illness.

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

2.2. Behavioural tasks

2.2.1. Cambridge Neuropsychological Test Automated Battery (CANTAB)

Four tasks were selected from the Cambridge Neuropsychological Test Automated Battery (CANTAB) (Cambridge Cognition, Cambridge UK version 5.0.0): '*Verbal Recognition Memory* (VRM),' '*Pattern Recognition Memory* (PRM),' '*Spatial Span* (SSP),' '*One Touch Stocking of Cambridge* (OTS).' All CANTAB tests were administered on a Windows operating system on a 15.6-inch touch-screen tablet computer. All participants first undertook a motor screen test to ensure participants were familiar with the concept of the touch-screen interface. Due to legal copyright restrictions, these clinical tests are owned by CANTAB and can only be accessed via the copyright holders. A brief outline of each task is provided below:

1. Verbal Recognition Memory (VRM) comprises of two phases. In the first phase, participants were shown a series of 12 neutral words which appeared on a screen one-by-one (some examples of similar words are: *prisoner, bud, golden, lake and infirmary*). These words were the same for each participant. Following the sequence, participants were asked to verbally recall as many words as possible from the list they had seen, with a maximum score (correctly recalled words) of 12. In the second phase of the task, participants were shown a sequence of 24 words (comprising of 12 original words that had appeared in the first phase, and 12 distractor words) and had to recognise the original words in a two-alternative forced-choice paradigm. Outcome measures in the first phase were the number of correctly recalled words and in the second phase, the number of correctly recognised original words.
2. Pattern Recognition Memory (PRM, see Fig. 1A) participants were shown two different series of 12 visual patterns which appeared in the centre of the screen in a continuous sequence one after the other. All participants were shown the same set of patterns. These patterns were novel and unfamiliar, comprising of lines which are designed so that they cannot easily be given verbal labels, nor did they look similar to common objects. In the first phase, participants were shown one series of 12 visual patterns, following which participants were presented with two options: one novel pattern and one pattern that had been presented during the continuous sequence. Participants had to indicate the previously presented pattern. This was repeated in the second phase of the task with a new set of patterns. In total, there were 24 trials and outcome measures were the number of correct trials.
3. Spatial Span (SSP, see Fig. 1B) participants were shown a number of white squares on a black screen which changed colour one-by-one in a variable sequence. The aim of the task was to remember and select the order in which various boxes changed colour in a sequence. The task increased in difficulty, with an increasing number of boxes in the sequence, from two boxes at the start to a maximum of nine. Each difficulty level was repeated three times, with a total of 24 trials. However, the task terminated when a participant failed to answer three consecutive trials correctly. On average, both participant groups answered between 21 and 24 trials (control mean = 20.85, SD = 1.81, and aphantasic mean 21.3, SD = 2.74), there were no significant differences in the number of trials completed between participant groups ($t(38) = 4.63$, $p = .54$, $d = .10$) Outcome measures were the span length (the longest sequence correctly recalled), number of errors and usage errors. The number of errors denotes the total number of times a participant pressed an incorrect box. The usage error is the number of times an incorrect box is pressed per sequence.
4. One Touch Stocking of Cambridge (OTS, see Fig. 1C), based on the Tower of Hanoi, participants were shown two arrangements of three coloured balls, one set positioned at the top, the other at the lower half of the screen. Each stocking had the capacity to hold three balls. The aim of the task was to rearrange the balls at the bottom of the screen in order to match the arrangement and the top of the screen. However, there were certain rules with regard to the way the balls could be moved. Participants had to calculate the minimum number of moves '*within their head*' and indicate their response. Participants were informed not to physically use any part of their bodies, for instance, their hands, fingers or head to aid the calculation of the minimum number of moves. In the most difficult trials, the maximum number of moves to solve the task was always 6. The results for move 1 were discounted in any analysis owing to the fact the test administrator was explaining instructions during this trial; thus, it increased the time taken to complete the trial. There were 20 trials in total, 4 trials per difficulty level, with five levels of difficulty. Outcome measures were the mean number of 'moves' (or attempts) to select a correct response (accuracy) and latency to correct (time taken to successfully complete the trial).

2.2.2. Mental rotation task (MRT)

Adapted from the classic Shepard and Metzler mental rotation experiment, stimuli were acquired from the Mental Rotation Stimulus library (Peters & Battista, 2008). All stimuli comprised of 10 cubes glued together in different orientations to form 'arms.' 138 white-cubed stimuli were selected, rotating around the x-axis with a full view (parts not occluded by parts of arms) were chosen from the Mental Rotation Stimulus library. Each stimulus was super-imposed on a black background for the task.

Based on the remaining angles, 6 levels of difficulty were chosen relative to 0°: 40°, 85°, 130°, 175°, 220°, 265°). Following an informal pilot of 12 participants, angle rotations of 130°, 175° and 265° were excluded as these angles had a higher accuracy relative to the 'easier' angles of rotation. As a result, three angles of rotation were selected; these were angles: 40°, 85°, and 220°. The task comprised of two blocks of 48 trials, forming 96 trials in total. One block (i.e., 48 trials) was included in each testing session of the study. The blocks were matched in terms of difficulty, with 16 trials per angle of rotation in each block and in terms of the number of same and different

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

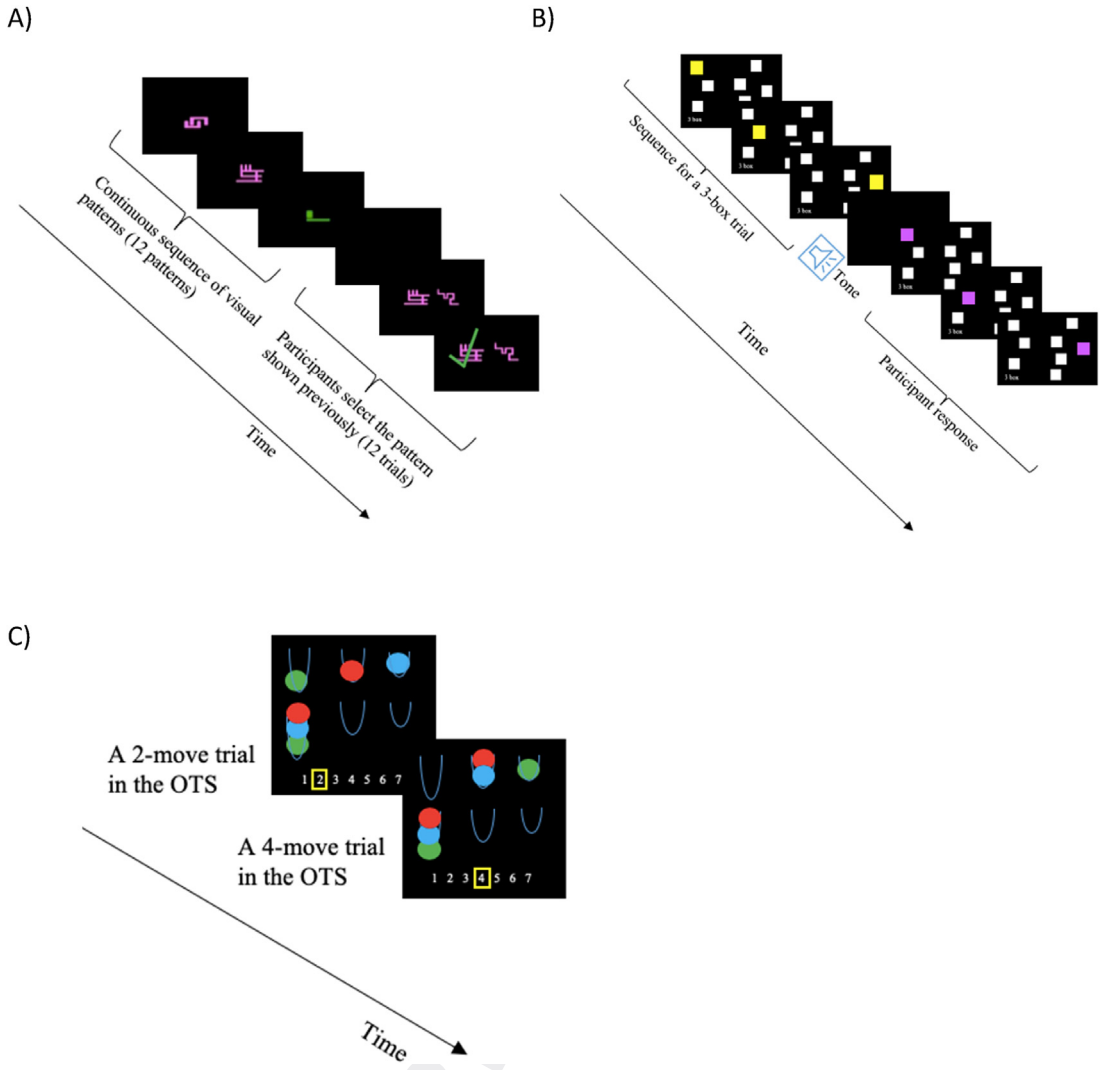

Fig. 1 – A) Diagram to show an example of the Pattern Recognition Memory (PRM). A continuous stream of visual patterns were presented, following which, participants selected the pattern they recognised. B) Diagram to show an example of a three-box trial in the Spatial Span (SSP). Participants were presented with a sequence of coloured boxes, and following the sound of a tone, selected the boxes as shown in the sequence. C) Diagram to show an example of a 2-move and 4-move trial in the One Touch Stocking of Cambridge (OTS). Participants needed to rearrange the bottom configuration of balls 'in their head' to match the top configuration and select the number referring to the minimum number of moves required.

responses. In each block of 48 trials, 24 stimuli were the same (i.e., the stimuli were of the shape, but displayed at a different orientation) and 24 were different. Of the 'different' trials, 23 were mirror images, while 25 trials were comprised of different images. The task was programmed on E-prime version 2, and outcome measures of performance were reaction time and accuracy (proportion of trials that were correct). The task materials are available (https://osf.io/q5t78/).

2.3. *Statistical analysis*

Participant characteristics, imagery questionnaires and neuropsychological tasks, data were analysed with two-way mixed ANOVAs and independent t-tests or the non-parametric equivalent, the Mann Whitney test, when normality assumptions were violated. All data transformations were undertaken in MATLAB.

Bayes Factors, assessing evidence in favour of the null hypothesis (BF01), were conducted to follow up statistical tests that were not statistically significant. These were calculated using JASP (https://jasp-stats.org/). For these analyses we used the rules of thumb outlined in Jeffereys (1961): BF1 = "*No evidence*", BFs 1–3 = "*Weak but positive evidence*", BFs 3–10 = "*Moderate evidence*", BFs 10–30 = "*Strong evidence*", BFs 30–100 = "*Very strong evidence*", and BFs > 100 = "*Extreme evidence*" to support the null hypothesis. Data visualisations represent the raw data not transformed data (see also Supplementary materials). We have provided data visualisations for the key analyses in the manuscript. Visualisations of all other analyses can be found in the Supplementary materials for the interested reader. All statistics analysed were performed with a significance level of $p < .05$, and all p values are two-tailed.

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

3. Results

3.1. Declarative memory tasks

3.1.1. Pattern Recognition Memory

In the PRM, a Mann–Whitney test was conducted as the data were not normally distributed, this showed that there was no evidence of a difference in performance (U = 179.5, p = .57, r = .09, BF_{01} = 2.85) between aphantasic (median of 22, range: 19–24) and control (median = 22, range: 19–24) participants (see Supplementary Fig. 1.1).

3.1.2. Verbal Recognition Memory

There was a ceiling effect in the recognition phase of the VRM (98–99% correct). As a result, only the free recall phase was analysed. In the free recall phase, an independent t-test showed that there was no difference in performance in free recall (t(38) = .11, p = .92, d = .02, BF_{01} = 3.20) between aphantasic (M = 7.4, SD = 1.7) and control (M = 7.5, SD = 1.82) participants (see Supplementary Fig. 1.2).

3.2. Visuo-spatial working memory

3.2.1. Spatial span

In the SSP, a Mann–Whitney test was conducted as the data were not normally distributed, this showed no evidence of a difference in memory spatial span (U = 170.5, p = .39, r = .14, BF_{01} = 2.60) between aphantasic (median = 7, range: 5–8) and control participants (median = 7, range: 6–8). Moreover, an independent t-test showed no significant difference in the total number of errors (the number of times an incorrect box was pressed across all trials) (t(38) = .47, p = .63, d = .16, BF_{01} = 2.95) between aphantasic (M = 14.1, SD = 4.61) and controls (M = 13.2, SD = 6.62) participants. For total usage error, an independent t-test showed no significant difference in the number of times a box was selected that was not in the span sequence for the trial (t(38) = .46, p = .65, d = .15, BF_{01} = 2.98) between aphantasic (M = 2.1, SD = 1.41) and control (M = 1.9, SD = 1.2) participants. These results show that the performance of individuals with aphantasia was comparable to individuals with typical imagery (see Supplementary Fig. 2.1).

3.2.2. One Touch Stocking of Cambridge

In the OTS, data were transformed using the Box–Cox transformation (Box & Cox, 1964) to address a violation of normality. Mean moves to correct is defined by the number of attempts a participant takes to opt for the correct response. Accuracy in the OTS was analysed for each number of moves from 2 moves to 6 moves using a two-way mixed measures ANOVA with factors participant group (aphantasic/control) and the number of moves (2–6). There was no significant main effect of participant group (F(1, 38) = .09, p = .76, ηp^2 = .002, $BF_{01} = 1.38e^{20}$), however, there was a significant main effect of number of moves (F(4, 152) = 36.63, p < .001, ηp^2 = .49). Post hoc tests using the Bonferroni correction for multiple comparisons revealed a significant pairwise difference in accuracy between all moves (p < .01) except (moves 2–3, 3–4, and 4–5, p > .09). There was no significant interaction between participant group and number of moves (F(4, 152) = .82, p = .52, ηp^2 = .02, BF_{01} = 9.24). These results suggest that the performance of individuals with aphantasia was comparable to individuals with typical imagery (see Supplementary Fig. 2.3).

Mean latency of correct responses is defined as the amount of time taken for participants to respond correctly within each trial-type. This was analysed using a two-way mixed ANOVA with Greenhouse–Geisser correction. The results of the two-way mixed ANOVA with factors participant group (aphantasic/control) and number of moves (2–6), showed that there no significant main effect of participant group (F(1, 38) = 1.90, p = .18, ηp^2 = .05, $BF_{01} = 6.90e^{71}$) but a significant main effect of number of moves (F(2.80, 106.43) = 287.17, p < .001, ηp^2 = .88). Post hoc tests using the Bonferroni correction for multiple comparisons revealed a significant pairwise difference in latency to correct for all moves 2–6 (p < .001). There was a significant interaction between participant group and the time taken across moves 2–6 (F(2.80, 106.43) = 3.40, p = .023, ηp^2 = .08). Subsequent follow up independent t-tests showed a significant difference in latency at moves 5 (t(38) = 2.65, p = .012, d = .78) and move 6 (t(38) = 2.62, p = .013, d = .76). However, this effect was not significant after Bonferroni correction (both move 5 and move 6, p = .060). All other moves (2–4) were not significant (p > .61). These results indicate a significant between the groups in the time taken to complete the task across the levels of task difficulty, likely driven by slower responses in the aphantasic group at higher levels of task difficulty, in which executive function demands could be expected to be highest (see Fig. 2). It should be noted, however, that within the sample of aphantasic participants there was great variation in terms of reaction time for moves 5 and moves 6 in the OTS, which suggests that some aphantasic participants were slower on the task than others participants.

3.2.3. Mental rotation (MRT)

The proportion correct MRT data was transformed using an arcsin transformation (Studebaker, 1985). The accuracy of mental rotation performance was first examined by angle of rotation between aphantasic and control participants using a two-way mixed measures ANOVA with Greenhouse–Geisser correction with a between-subject factor of group (aphantasic/control) and within-subject factor of the angle of rotation (40°, 85°, and 220°). There was a significant main effect of angle of rotation (F(1.70, 64.7) = 29.92, p < .001, ηp^2 = .44). Post hoc tests using the Bonferroni correction for multiple comparisons revealed a significant pairwise difference in accuracy between all angles (p < .04). There was no main effect of group (F(1, 38) = .76, p = .39, ηp^2 = .02, $BF_{01} = 1.13e^{8}$) and no significant interaction between the angle of rotation and group (F(1.70, 64.7) = .29, p = .72, ηp^2 = .008, BF_{01} = 6.07). These results show that despite self-reporting a lack of visual imagery, participants with aphantasia do not significantly differ from participants with typical imagery on this task.

Reaction time data for the MRT was transformed using the Box–Cox transformation to meet normality assumptions (Box & Cox, 1964). Reaction time data was analysed by angles of rotation (40°, 85°, and 220°) and compared between groups. The data was analysed using a two-way mixed ANOVA with Greenhouse–Geisser corrections. The results of the two-way mixed measures ANOVA with between-subject factor group

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

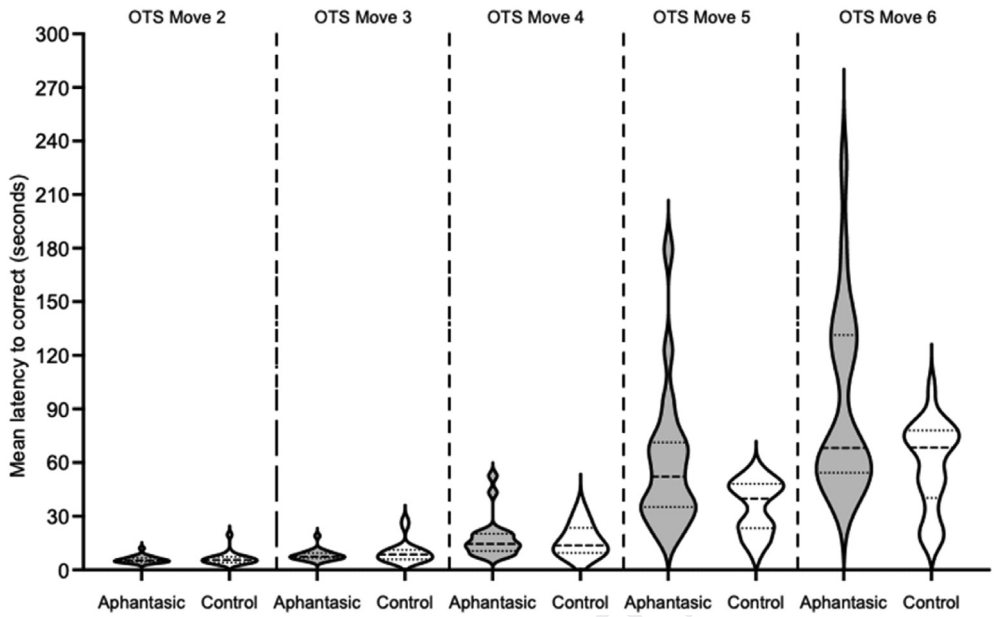

Fig. 2 – Raw data violin graph (overall distribution, median and interquartile range) showing latency to correct (response time in seconds) for each move in the OTS between control and aphantasic participants.

(aphantasic/control) and within-subject factor angle of rotation (40°, 85°, and 220°), showed a significant main effect of angle of rotation on reaction time ($F(1.65, 62.86) = 66.22$, $p < .001$, $\eta p^2 = .64$). Post hoc tests using the Bonferroni correction for multiple comparisons revealed a significant pairwise difference in reaction time between all angles ($p < .01$). There was no significant main effect of group ($F(1, 38) = 3.62$, $p = .07$, $\eta p^2 = .087$, $BF_{01} = 2.29e^{14}$) and no significant interaction between angle of rotation and group ($F(1.65, 62.86) = .45$, $p = .60$, $\eta p^2 = .012$, $BF_{01} = 4.80$). This result show that participants with aphantasia take the same amount of time to respond in the MRT similar to participants with typical imagery (see Supplementary Fig. 2.2).

4. Severity of aphantasia as measured by the VVIQ

To assess whether the findings in this study were affected by our VVIQ cut-off criteria, all task performance was reanalysed only including aphantasic participants with a VVIQ score of 16 (n = 17), compared to control participants (n = 20, see Supplementary materials for full analysis per task). In summary, there were no differences to the performance as outlined above, except in the response time for the mental rotation task. In this task, there was a main effect of group, that was significant when considering this more severe subgroup (i.e., aphantasic participants who scored 16 on the VVIQ), which had not been significant when considering the full group ($F(1, 35) = 5.13$, $p = .03$, $\eta p^2 = .13$) (see Supplementary materials for the remaining analysis). This finding suggests that the severity of aphantasia (and VVIQ criterion) is important to consider within studies which explore behavioural performance between individuals with different imagery experiences.

5. Discussion

This study examined the performance of a modest sample of individuals with congenital aphantasia within a battery of neuropsychological declarative memory and visual working memory tasks. On the declarative memory tasks (the VRM and PRM), there were no differences between aphantasic individuals and those with typical imagery. In other words, aphantasic individuals did not appear to have either a general declarative memory impairment nor one that is specific to visual declarative memory. In the visuo-spatial working memory tasks, there were differences between the groups on the OTS but not the SSP task. Given the similar performance on the SSP, this suggests that the capacity for and ability to maintain visuo-spatial information in memory in aphantasic participants does not differ overtly to that of typical imagers. Differences were evident however in the OTS and the MRT, tasks that included additional manipulation, planning and executive function components. In the case of the MRT, this difference was only evident in the most severely impaired participants (those who scored the minimum of 16 on the VVIQ) and not in the full sample. These small group differences found only in the more cognitive demanding tasks were evident in response time and not task accuracy. Hence, considered together, our results suggest that despite differences in the subjective experience of visual imagery, aphantasic individuals do not show significant impairments in visual working memory or declarative memory that are likely to hamper everyday life.

In terms of standard lab-based recall and recognition tasks, our results are in line with Milton et al. (2021) in showing no differences in performance between aphantasic and typical imager participants. This is in contrast to the self-reported deficits in both episodic memory (Dawes et al., 2020) and

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

autobiographical memory (Milton et al., 2021). However, while both the declarative memory tasks (used here) and the self-reports (e.g., Dawes et al., 2020) concern memory for an episode, the self-reports more specifically probe the retrieval of experience or specific aspects of previous events or scenes from one's life. In comparison, lab-based recall and recognition tasks probe the retrieval of learned experimental material. While both are generally considered episodic memory, they are shown to engage different brain regions (Chen, Gilmore, Nelson, & McDermott, 2017; Roediger & McDermott, 2013). Autobiographical retrieval of life events is shown to activate the default mode network, whereas the retrieval of recently encountered experimental material within lab-based episodic memory tasks is shown to activate frontal parietal regions (Chen et al., 2017; McDermott, Szpunar, & Christ, 2009). This suggests that there are differing forms of episodic memory (i.e., memory of retrieval of life events and memory of recently learned material), which are underpinned by differing neural networks and processes (Chen et al., 2017; Roediger & McDermott, 2013). This distinction within episodic memory may be further explored within aphantasia, whereby preliminary evidence through self-reports suggest impairment in episodic autobiographical memory retrieval, but not episodic retrieval of experimental materials. At the same time, it should be noted that not all aphantasic individuals report difficulties with autobiographical memory (Zeman et al., 2020). Further research is required to examine differences in episodic memory experience in aphantasia.

The lack of differences in performance in the SSP between participants with aphantasia and typical imagery is perhaps surprising, given the previously reported relationship between imagery strength and visual working memory capacity (Keogh & Pearson, 2014). There could be two explanations for this. Firstly, it could be that aphantasic participants are using the same unimpaired processes that typical imagers use. Alternatively, it could be that aphantasic participants use a different non-visual process or specific strategy, that results in similar performance levels. Hence, as with all tasks in this study it remains unclear whether aphantasic participants are achieving similar levels of accuracy in tasks involving imagery via the same or different routes to those with typical imagery. We did not explicitly ask participants how they performed each task. Indeed, it is difficult for participants to accurately introspect on the cognitive processes that they have used to perform a task, particularly when those processes may operate at an unconscious level. In the future it may be possible to design studies to block hypothesised alternative routes e.g., reliance on verbal or spatial codes (cf Jacobs, Schwarzkopf, & Silvanto, 2018), as a means to better understand the mechanisms that aphantasic individuals use in imagery tasks.

Similarly, for the MRT, the lack of significant difference in accuracy mirrored performance by patient *MX* (Zeman et al., 2010). Considering the full sample (comprising VVIQ scores between 16 and 24), a lack of group difference for reaction time were apparent. However, in the sample of aphantasic participants who only scored 16 on the VVIQ, there was a significant group difference in reaction time in the MRT, which similar to patient MX (who also scored 16 on the VVIQ) and showed longer reaction times in the MRT (Zeman et al., 2010). This might suggest that the severity of aphantasia and the cut-offs adopted within studies are important and objective deficits are dependent on the severity of aphantasia. However, this finding needs to be interpreted with caution given the number of additional tests that were conducted to analyse this sub-group. Zeman et al. (2010) reported that the slower response times exhibited by MX were due to the use of a different strategy in the task, and aphantasic participants report using non-visual strategies, which are functionally equivalent to visual imagery, within visual working memory paradigms (Keogh, Wicken & Pearson, 2021). Tasks such as the SSP and MRT are suggested to load more heavily on spatial imagery, with studies documenting that aphantasic participants self-report intact spatial imagery abilities (Bainbridge et al., 2020; Dawes et al., 2020; Keogh & Pearson, 2018). The behavioural mental rotation data suggests that both participants with aphantasia and typical imagery showed an increase in response time with increase in angle of rotation within the mental rotation task, suggesting the use of analogical strategies. Further, tasks such as mental rotation are reported to not rely on visual, but spatial representations (Liesefeld & Zimmer, 2013). Evidence from the congenitally blind literature suggests that some imagery tasks, such as mental rotation, can be undertaken as accurately in the absence of a 'visual' component (e.g., Carpenter & Eisenberg, 1978; Eardley & Pring, 2007; Marmor & Zaback, 1976), however, congenitally blind individuals take longer to respond in mental rotation tasks compared to sighted individuals (Kerr, 1983). This is similar to the performance exhibited by the sub-group of aphantasic participants who self-reported a severe visual imagery deficit on the VVIQ. This suggests that aphantasic participants may be using non-visual processes such as spatial imagery in these tasks, similar to congenitally blind individuals. Further research exploring task performance should also include measures of response time (not only accuracy) to further explore differences between groups.

Alternatively, MRT Tasks have been shown to activate motor areas (such as the premotor cortex and supplementary motor area) and this is thought to reflect the use of motor simulation within tasks (e.g., Logie, Pernet, Buonocore, & Della Sala, 2011; Zacks, 2008). Activation of the premotor cortex is suggested to be related to object rotations while the supplementary motor area (SMA) is related to rotation of the self. In a study exploring the brain activation of high and low vivid imagers, individuals who were classified as low imagers were less accurate in a mental rotation task (with no differences in response time) (Logie et al., 2011). The authors suggested that this may be because low imagers were using a self-referential strategy, as supported by the greater activation in SMA areas compared to high imagers, who showed greater activation the premotor cortex (Logie et al., 2011). The authors suggested that the low imagers' use of the self-referential strategy was due to their difficulties in representing images of external objects, which resulted in less accurate performance in the task. While in contrast in the current study, no differences in accuracy were evident in the MRT between participants who self-report an absence of imagery compared to and those with typical imagery. Given this similarity in performance, but contrast in self-reported visual imagery experience, further research should explore differences in brain activation within tasks such as the MRT to confirm whether the processes

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

adopted by individuals with aphantasia are comparable to typical imagers.

While few differences in performance were evident within tasks within the current study, differences have been documented on objective tasks such as in imagery priming in binocular rivalry and by fewer object details drawn in a visual memory paradigm (Bainbridge et al., 2020; Keogh & Pearson, 2018). This suggests these tasks load more on the requirement and experience of visual representations, however, it should be noted that no drawing differences in spatial details were apparent between individuals with aphantasia and typical imagery (Bainbridge et al., 2020). Neuroimaging, neuropsychological case studies and individual differences research have demonstrated the dissociation between visual-object and visual-spatial imagery, and these imagery subtypes are underpinned by functionally and anatomically separate processing pathways – the ventral and dorsal pathways, respectively (e.g., Blajenkova, Kozhevnikov, & Motes, 2006; Carlesimo, Perri, Turriziani, Tomaiuolo, & Caltagirone, 2001; Farah, 1984; Farah, Levine, & Calvanio, 1988; Kozhevnikov, Hegarty, & Mayer, 2002; Kozhevnikov, Kosslyn, & Shephard, 2005).

Although these results did not show a blanket deficit with the planning components of the OTS task, significantly slower performance suggests that the self-reported lack of visual imagery may be impacting performance. Further, descriptively the results suggest that the trials where aphantasic performance was slower than typical imagers were trials associated with instances of high working memory load and manipulation of visuo-spatial information (i.e., at move 5 and move 6). Although participants were told not to use body gestures within the task, participants were not told to refrain from making covert eye movements. Whether participants used covert eye movements remains unclear, however, it has been suggested that there are differences in eye gaze between individuals who make errors compared to those that are efficient in the task (Hodgson, et al., 2000). While eye movement control and imagery are suggested to be closely linked (e.g., Bone et al., 2019; Brandt & Stark, 1997; Fortassi, Rode & Pisella, 2017), specifically the use of strategic eye movements in relation to imagery in the OTS are mixed. On one hand it is suggested that the maintenance of external representations through eye movements interferes with the imagery processes during the OTS (Hodgson, et al., 2000). However, eye movements are also thought to allow imagery representations to be 'scaffolded' upon sensory representations during cognitive planning, thus reducing the load on imagery requirements (Clark, 1997). Further research should examine the strategic use of eye movements in more detail with eye-tracking.

In terms of the multicomponent working memory, it has been suggested that in scenarios where highly detailed visual details are required to be maintained, it may involve the repeat generation of the image within the visual buffer, rather than maintenance of visual information in the visual cache (Darling, Della Sala, & Logie, 2009; Kosslyn & Thompson, 2003). In contrast, during low load working memory trials, which are suggested to comprise of the maintenance and manipulation of no more than four balls (Fukuda, Awh, & Vogel, 2010), there were no differences in performance between aphantasic and control participants with typical imagery. This suggests that the processes that the aphantasic participants adopted in the task were conducive only up to a certain level, with increasing manipulation and working memory load resulting in significant group differences in reaction time (with no differences in accuracy). This pattern of performance is similar to that exhibited by congenitally blind individuals who show longer reaction times in imagery tasks (e.g., Carpenter & Eisenberg, 1978; Kerr, 1983; Zimler & Keenan, 1983) as they are suggested to have a lower visuo-spatial processing capacity compared to sighted individuals (Vecchi, 1998; Vecchi, Monticellai, & Cornoldi, 1995).

While the data presented here is purely behavioural, it is nevertheless worthwhile to consider its implications to the understanding of the neural basis of imagery, in particularly in relation to working memory and visual perception. The dominant view is that imagery and visual working memory engage the same areas and neurons which are activated by visual stimulation; this is known as the sensory recruitment hypothesis (Postle, 2006; D'Esposito, 2007). This view is supported by numerous imaging studies showing that imagery and working memory content can be decoded from same areas of visual cortex which underlie visual perception (e.g., Albers et al., 2013). However, a limitation in decoding studies is whether what is being decoded reflects memory for the stimulus rather than actual imagery content. A study which controlled for this found no V1 involvement in imagery (Muckli et al., 2005). There is also much evidence inconsistent with this view (see Bartolomeo, Hajhajate, Liu, & Spagna, 2020). For example, Slotnick et al. (2005) found that a high-resolution visual imagery task can induces topographically organized activity in striate cortex, but this was found only in half of the participants. Furthermore, some patients with a lesion to primary visual cortex continue to have visual imagery (Chatterjee & Southwood, 1995). Very recently, a large-scale meta-analysis of 46 fMRI studies found no evidence for imagery-related activity in early visual cortices (Spagna et al., 2021). Furthermore, behaviourally it has been shown that performance in visual working memory can be predicted by the strength of mental imagery (Keogh and Pearson; 2011, see also Berger and Gaunitz, 1979) however, this was only found for individuals who rated themselves being good imagers, indicating the existence of different strategies in those with poor imagery. The present results appear to be in contradiction with this view, as the absence of visual imagery had very little impact on visual memory tasks. Thus, there appears to be more to visual imagery than the engagement of overlapping visual areas (as proposed by the sensory recruitment hypothesis) given that working memory functions can survive the absence of visual imagery. Another possibility is that while imagery engages visual cortex, additional brain regions are also required. This issue requires further neuroimaging studies to be resolved.

It is also worth noting that our sample size was relatively modest, although larger than many other in-person behavioural studies with aphantasic participants (Keogh & Pearson, 2017). Consequently, it is possible that neuropsychological task differences may have been found if a larger sample had been used. Recruiting aphantasic participants can be difficult. In the future, studies using online behavioural tasks may help

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

to boost recruitment. It is also important to acknowledge the limitations resulting from the fact that aphantasia is a condition defined using subjective measures (i.e., the VVIQ questionnaire). For example, interpretation of what it means to have a vivid mental image may very well differ between participants – a vivid mental image for one person might be a weak one for another. As there are currently no objective measures for aphantasia, this issue is difficult to resolve and it is indeed possible that some of the null effects reported here are due some of the participants in the aphantasic group not being "true" aphantasics. A promising avenue is the use of tasks such as priming by binocular rivalry which is reduced in aphantasia (Keogh & Pearson, 2018). However, such tasks do not seem yet to be diagnostic at an individual level. Alternatively, measuring pupillary light responses has been proposed to be a physiological way to objectively identifying aphantasic individuals within samples (Kay, Keogh, Andrillion, & Pearson, 2021).

Nevertheless, this research highlights a notable contrast between the self-reported impaired experience of imagery and the largely unimpaired performance on objective measures looking at aspects of cognition thought to be involved in the imagery process. A potential explanation for the difference in the magnitude of effect may lie in recent research that has identified variation in the experience of aphantasia, such as the variation in sensory imagery experience (e.g., Dance et al., 2021; Dawes et al., 2020; Zeman et al., 2020), raising the possibility that there may be subtypes of aphantasia (i.e., aphantasia is unlikely to be a homogenous experience). Within the current study, there was substantial variation in response times during the difficult trials of the OTS task. While this may be anomalous performance or 'noise' within the data, this also might suggest that aphantasic participants are using different processes or some using more efficient strategies to complete the tasks. Arguably, it raises the possibility that at least some aphantasic individuals, may retain the ability to generate visual imagery, but lack conscious access to this imagery. These aphantasic participants may be able to use the visual buffer to regenerate the complex configurations (Darling et al., 2009) required with the OTS task (similar to individuals with typical imagery), despite this re-generation process occurring outside of conscious awareness. Future studies should explore individual differences to further identify variations in behavioural performance.

6. Conclusion

Despite their difference in self-reported conscious experience of visual imagery, individuals with aphantasia performed as accurately as individuals with typical imagery on a number of neuropsychological tasks exploring declarative and visuospatial working memory. The only exceptions were differences in response time for aphantasic individuals relative to typical imagers in the OTS task, likely at higher levels of task difficulty. Secondly, a significant group difference in response time in the MRT, however, this difference was only evident within the sub-group of aphantasic participants who reported a severe visual imagery deficit. Based on the evidence of slower performance, it is the possible that aphantasic individuals are completing these tasks without access to visual imagery, but rather by using spatial imagery (similar to congenitally blind individuals). Alternatively, this could be explained by the fact that aphantasic individuals lack conscious awareness of their visual imagery experience. These findings suggest the importance of collecting response time data to indicate the use of alternative processes in tasks. The sample size did not permit exploration of individual differences. Ultimately, the results suggest that despite the differences in the subjective experience of visual imagery, aphantasic individuals do not show significant impairments in visual working memory or declarative memory that would hamper everyday life.

Funding

Participant payment was funded by The European Research Council awarded to JS, grant number: 336152. Q6

CRediT authorship contribution statement

Z. Pounder: Study Conceptualization, Methodology, Investigation, Project administration, Software, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization; **J. Jacob**: Conceptualization, Methodology, Software, Writing – review & editing; **S. Evans:** Resources, Software, Writing – review & editing; **C. Loveday**: Conceptualization, Methodology, Writing – review & editing; **A. Eardley:** Writing – review & editing; **J. Silvanto:** – Conceptualization, Methodology, Funding acquisition, Writing – review & editing.

Open practices

The study in this article earned an Open Data badge for transparent practices. Data from this study can be found at: https://osf.io/xzmub.

Acknowledgements

We would like to greatly thank all of our aphantasic and typical imager participants who took the time to undertake this study.

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2021.12.010.

Uncited references Q8

Dance et al., 2021a; Kaas et al., 2010.

REFERENCES

Alibali, M., Spencer, R., Knox, L., & Kita, S. (2011). Spontaneous gestures influence strategy choices in problem solving. *Psychological Science, 22*(9), 1138–1144. https://doi.org/10.1177/0956797611417722. Journals.Sagepub.Com.

Bainbridge, W. A., Pounder, Z., Eardley, A. F., & Baker, C. I. (2020). Quantifying aphantasia through drawing: Those without visual imagery show deficits in object but not spatial memory. *Cortex, 135*, 159–172. https://doi.org/10.1016/j.cortex.2020.11.014

Bartolomeo, P. (2002). The relationship between visual perception and visual mental imagery: A reappraisal of the neuropsychological evidence. *Cortex, 38*(3), 357–378. https://doi.org/10.1016/s0010-9452(08)70665-8

Bartolomeo, P., Hajhajate, D., Liu, J., & Spagna, A. (2020). Assessing the causal role of early visual areas in visual mental imagery. *Nature Reviews. Neuroscience, 21*(9), 517. https://doi.org/10.1038/s41583-020-0348-5

Blajenkova, O., Kozhevnikov, M., & Motes, M. A. (2006). Object-spatial imagery: A new self-report imagery questionnaire. *Applied Cognitive Psychology, 20*, 239–263.

Bone, M. B., St-Lauret, M., Dang, C., McQuiggan, D. A., Ryan, J. D., & Buchsbaum, B. R. (2019). Eye movement reinstatement and neural reactivation during mental imagery. *Cerebral Cortex, 29*(3), 1075–1089. https://doi.org/10.1093/cercor/bhy014

Box, G. E. P., & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal statistical Society. Series B (methodological), 26*. Retrieved from http://about.jstor.org/terms.

Brandt, S. A., & Stark, L. W. (1997). Spontaneous eye movements during visual imagery reflect the content of the visual scene. *Journal of Cognitive Neuroscience, 9*(1), 27–38. https://doi.org/10.1162/jocn.1997.9.1.27

Carlesimo, G., Perri, R., Turriziani, P., Tomaiuolo, F., & Caltagirone, C. (2001). Remembering what but not where: Independence of spatial and visual working memory in the human brain. *Cortex, 37*(4), 519–534. https://doi.org/10.1016/S0010-9452(08)70591-4

Carpenter, P., & Eisenberg, P. (1978). Mental rotation and the frame of reference in blind and sighted individuals. *Perception & Psychophysics, 23*(2), 117–124. https://doi.org/10.3758/bf03208291

Chen, H. Y., Gilmore, A. W., Nelson, S. M., & McDermott, K. B. (2017). Are there multiple kinds of episodic memory? An fMRI investigation comparing autobiographical and recognition memory tasks. *Journal of Neuroscience, 37*(10), 2764–2775. https://doi.org/10.1523/JNEUROSCI.1534-16.2017

Clark, A. (1997). *Being there: Putting brain, body and world together again*. Cambridge: MIT Press.

Dance, C. J., Jaquiery, M., Eagleman, D. M., Porteous, D., Zeman, A., & Simner, J. (2021a). What is the relationship between aphantasia, synaesthesia and autism? *Consciousness and Cognition, 89*, 103087. https://doi.org/10.1016/j.concog.2021.103087

Dance, C. J., Ward, J., & Simner, J. (2021b). What is the link between mental imagery and sensory sensitivity? Insights from aphantasia. *Perception, 50*(9), 757–782. https://doi.org/10.1177/03010066211042186

Darling, S., Della Sala, S., & Logie, R. H. (2009). Segregation within visuo-spatial working memory: Appearance is stored separately from location. *Quarterly Journal of Experimental Psychology, 62*, 417–425. https://doi.org/10.1007/s10339-007-0171-1

Dawes, A. J., Keogh, R., Andrillon, T., & Pearson, J. (2020). A cognitive profile of multi-sensory imagery, memory and dreaming in aphantasia. *Scientific Reports, 10*(1), 1–10. https://doi.org/10.1038/s41598-020-65705-7

Eardley, A. F., & Pring, L. (2007). Spatial processing, mental imagery, and creativity in individuals with and without sight. *European Journal of Cognitive Psychology, 19*(1), 37–58. https://doi.org/10.1080/09541440600591965

Eielts, C., Pouw, W., Ouwehand, K., van Gog, T., Zwaan, R. A., & Paas, F. (2020). Co- thought gesturing supports more complex problem solving in subjects with lower visual working-memory capacity. *Psychological Research, 84*(2), 502–513. https://doi.org/10.1007/s00426-018-1065-9

Farah, M. J. (1984). The neurological basis of mental imagery: A componential analysis. *Cognition, 18*(1–3), 245–272.

Farah, M. J., Levine, D. N., & Calvanio, R. (1988). A case study of mental imagery deficit. *Brain and Cognition, 8*(2), 147–164. https://doi.org/10.1016/0278-2626(88)90046-2

Faw, B. (2009). Conflicting intuitions may be based on differing abilities - evidence from mental imaging research. *Journal of Consciousness Studies, 16*, 45–68.

Foster, J. J., Bsales, E. M., Jaffe, R. J., & Awh, E. (2017). Alpha-band activity reveals spontaneous representations of spatial position in visual working memory. *Current Biology, 27*(20), 3216–3223. https://doi.org/10.1016/j.cub.2017.09.031. e6.

Fourtassi, M., Rode, G., & Pisella, L. (2017). Using eye movements to explore mental representations of space. *Annals of Physical and Rehabilitation Medicine, 60*(3), 160–163. https://10.1016/j.rehab.2016.03.001.

Fukuda, K., Awh, E., & Vogel, E. K. (2010, April 1). Discrete capacity limits in visual working memory. *Current Opinion in Neurobiology, 20*, 177–182. https://doi.org/10.1016/j.conb.2010.03.005

Galton, F. (1880). Statistics of mental imagery. *Mind, 5*, 301–318.

Hodgson, T., Bajwa, A., Owen, A., & Kennard, C. (2000). The strategic control of gaze direction in the tower of London task. *Journal of Cognitive Neuroscience, 12*(5), 894–907. https://doi.org/10.1162/089892900562499

Jacobs, C., Schwarzkopf, D. S., & Silvanto, J. (2018). Visual working memory performance in aphantasia. *Cortex, 105*, 61–73. https://doi.org/10.1016/j.cortex.2017.10.014

Jeffreys, H. (1961). *Theory of Probability*. Clarendon Press.

Kaas, A., Weigelt, S., Roebroeck, A., Kohler, A., & Muckli, L. (2010 Jan 1). Imagery of a moving object: The role of occipital cortex and human MT/V5+. *Neuroimage, 49*(1), 794–804. https://doi.org/10.1016/j.neuroimage.2009.07.055. Epub 2009 Jul 29. PMID: 19646536.

Kay, L., Keogh, R., Andrillion T., & Pearson, J. (2021). The eyes have it: The pupillary light response as a physiological index of aphantasia, sensory and phenomenological imagery strength https://doi.org/10.1101/2021.09.02.457617. Q7

Keogh, R., & Pearson, J. (2014). The sensory strength of voluntary visual imagery predicts visual working memory capacity. *Journal of Vision, 14*(12). https://doi.org/10.1167/14.12.7, 7–7.

Keogh, R., & Pearson, J. (2018). The blind mind: No sensory visual imagery in aphantasia. *Cortex, 105*, 53–60. https://doi.org/10.1016/j.cortex.2017.10.012

Keogh, R., & Pearson, J. (2021). Attention driven phantom vision: Measuring the sensory strength of attentional templates and their relation to visual mental imagery and aphantasia. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 376*(1817), 20190688. https://doi.org/10.1098/rstb.2019.0688

Keogh, R., Pearson, J., & Zeman, A. (2021a). Aphantasia: The science of visual imagery extremes. *Handbook of Clinical Neurology, 178*, 277–296. https://doi.org/10.1016/B978-0-12-821377-3.00012-X

Keogh, R., Wicken, M., & Pearson, J. (2021b). Visual working memory in aphantasia: Retained accuracy and capacity with a different strategy. *Cortex, 143*, 237–253. https://doi.org/10.1016/j.cortex.2021.07.012

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010

Kerr, N. (1983). The role of vision in "visual imagery" experiments: Evidence from the congenitally blind. *Journal of Experimental Psychology: General, 112*(2), 265–277.

Konigsmark, V. T., Bergmann, J., & Reeder, R. R. (2021). The Ganzflicker experience: High probability of seeing vivid and complex pseudo-hallucinations with imagery but not aphantasia. *Cortex, 141*, 522–534. https://doi.org/10.1016/j.cortex.2021.05.007

Kosslyn, S., & Thompson, W. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin, 129*(5), 723–746. https://doi.org/10.1037/0033-2909.129.5.723

Kozhevnikov, M., Hegarty, M., & Mayer, R. (2002). Revising the visualizer-verbalizer dimension: Evidence for two types of visualizers. *Cognition and Instruction, 20*(1), 47–77. Retrieved from http://www.jstor.org/stable/3233862.

Kozhevnikov, M., Kosslyn, S., & Shephard, J. (2005). Spatial versus object visualizers: A new characterization of visual cognitive style. *Memory & Cognition, 33*(4), 710–726.

Levaux, M. N., Potvin, S., Sepehry, A. A., Sablier, J., Mendrek, A., & Stip, E. (2007). Computerized assessment of cognition in schizophrenia: Promises and pitfalls of CANTAB. *European Psychiatry, 22*(2), 104–115. https://doi.org/10.1016/J.EURPSY.2006.11.004

Liesefeld, H. R., & Zimmer, H. D. (2013). Think spatial: The representation in mental rotation is nonvisual. *Journal of Experimental Psychology: Learning Memory and Cognition, 39*(1), 167–182. https://doi.org/10.1037/a0028904

Logie, R. H., Pernet, C. R., Buonocore, A., & Della Sala, S. (2011). Low and high imagers activate networks differentially in mental rotation. *Neuropsychologia, 49*(11), 3071–3077. https://doi.org/10.1016/J.Neuropsychologia.2011.07.011

Marmor, & Zaback. (1976). Mental rotation by the blind: Does mental rotation depend on visual imagery? *Journal of Experimental Psychology. Human Perception and Performance, 2*(4), 515–521.

Mathias, J., Bowden, S., & Barrett-Woodbridge, M. (2007). Accuracy of the Wechsler test of Adult reading (WTAR) and national adult reading test (NART) when estimating IQ in a healthy Australian sample. *Australian Psychologist, 42*(1), 49–56. https://doi.org/10.1080/00050060600827599

McCants, C. W., Katus, T., & Eimer, M. (2019). The capacity and resolution of spatial working memory and its role in the storage of non-spatial features. *Biological Psychology, 140*, 108–118. https://doi.org/10.1016/j.biopsycho.2018.12.006

McDermott, K. B., Szpunar, K. K., & Christ, S. E. (2009). Laboratory-based and autobiographical retrieval tasks differ substantially in their neural substrates. *Neuropsychologia, 47*(11), 2290–2298. https://doi.org/10.1016/j.neuropsychologia.2008.12.025

McKelvie, S. J. (1995). The VVIQ as a psychometric test of individual differences in visual imagery vividness: A critical quantitative review and plea for direction. *Journal of Mental Imagery, 19*(3–4), 1–106.

McKelvie, S. J., & Demers, E. G. (1979). Individual differences in reported visual imagery and memory performance. *British Journal of Psychology, 70*(1), 51–57.

Milton, F., Fulford, J., Dance, C., Gaddum, J., Heuerman-Williamson, B., Jones, K., et al. (2021). Behavioral and neural signatures of visual imagery vividness extremes: Aphantasia vs. Hyperphantasia. *Cerebral Cortex Communications, 2*(2), 1–15. https://doi.org/10.1093/texcom/tgab035

Monzel, M., Keidel, K., & Reuter, M. (2021). Imagine, and you will find – lack of attentional guidance through visual imagery in aphantasics. *Attention, Perception & Psychophysics, 83*(6), 2486–2497. https://doi.org/10.3758/s13414-021-02307-z

Patt, V. M., Thomas, M. L., Minassian, A., Geyer, M. A., Brown, G. G., & Perry, W. (2014). Disentangling working memory processes during spatial span assessment: A modeling analysis of preferred eye movement strategies. *Journal of Clinical and Experimental Neuropsychology, 36*(2), 186–204. https://doi.org/10.1080/13803395.2013.877123

Peters, M., & Battista, C. (2008). Applications of mental rotation figures of the Shepard and Metzler type and description of a mental rotation stimulus library. *Brain and Cognition, 66*, 260–264. https://doi.org/10.1016/j.bandc.2007.09.003

Roediger, H. L., & McDermott, K. B. (2013, December 24). Two types of event memory. *Proceedings of the National Academy of Sciences of the United States of America, 110*, 20856–20857. https://doi.org/10.1073/pnas.1321373110

Shepard, R., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science, 171*(3972), 701–703.

Squire, L. R. (1992). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience, 4*(3), 232–243.

Studebaker, G. (1985). A "rationalized" arcsine transform. *Journal of Speech, Language, and Hearing Research, 28*(3), 455–462.

Vecchi, T. (1998). Visuo-spatial imagery in congenitally totally blind people. *Memory, 6*(1), 91–102. https://doi.org/10.1080/741941601

Vecchi, T., Monticellai, M., & Cornoldi, C. (1995). Visuo-spatial working memory: Structures and variables affecting a capacity measure. *Neuropsychologia, 33*(11), 1549–1564.

Wechsler, D. (2001). *Wechsler test of adult reading: WTAR*. San Antonio, TX: Psychological Corporation.

Wicken, M., Keogh, R., & Pearson, J. (2021). The critical role of mental imagery in human emotion: Insights from fear-based imagery and aphantasia. *Proceedings of the Royal Society B: Biological Sciences, 288*(1946), 20210267. https://doi.org/10.1098/rspb.2021.0267

Xue, J., Li, C., Quan, C., Lu, Y., Yue, J., & Zhang, C. (2017). Uncovering the cognitive processes underlying mental rotation: An eye-movement study. *Scientific Reports, 7*(1), 1–12. https://doi.org/10.1038/s41598-017-10683-6

Zacks, J. M. (2008). Neuroimaging studies of mental rotation: A meta-analysis and review. *Journal of Cognitive Neuroscience, 20*(1), 1–19. https://doi.org/10.1162/jocn.2008.20013

Zeman, A., Della Sala, Torrens, L., Gountouna, V., McGonigle, D., & Logie, R. (2010). Loss of imagery phenomenology with intact visuo-spatial task performance: A case of "blind imagination. *Neuropsychologia, 48*(1), 145–155. https://doi.org/10.1016/j.neuropsychologia.2009.08.024

Zeman, A., Dewar, M., & Della-Sala, S. (2015). Lives without imagery – congenital aphantasia. *Cortex, 73*, 378–380. https://doi.org/10.1016/j.cortex.2015.05.019

Zeman, A., Milton, F., Della Sala, S., Dewar, M., Frayling, T., Gaddum, J., et al. (2020). Phantasia – The psychological significance of lifelong visual imagery vividness extremes. *Cortex*. https://doi.org/10.1016/j.cortex.2020.04.003

Zimler, J., & Keenan, J. (1983). Imagery in the congenitally blind: How visual are visual images? *Journal of Experimental Psychology. Learning, Memory, and Cognition, 9*(2), 269–282.

Please cite this article as: Pounder, Z et al., Only minimal differences between individuals with congenital aphantasia and those with typical imagery on neuropsychological tasks that involve imagery, Cortex, https://doi.org/10.1016/j.cortex.2021.12.010