



Article

Lateral Bias in Visual Working Memory

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Highlights:

What are the main findings?

- Greater performance in men and women when letters presented in RVF.
- Smaller asymmetry related to better performance for women but not men.

What is the implication of the main finding?

- Lateral bias in visual working memory was independent from lateralization of lexical decisions.

Abstract: The present study aimed to evaluate functional cerebral asymmetries of visual working memory (VWM) in relation to language lateralization. The bilateral change detection paradigm with capital letters as stimuli and the translingual lexical decision task were used to assess VWM and language asymmetry, respectively, in a sample of 99 younger healthy participants (59 women). Participant attention was cued towards right or left visual half-field. For the VWM task, men and women were more accurate and faster when stimuli were presented in the right visual half-field compared to the left visual half-field. As expected, a significant right visual half-field advantage was demonstrated in the lexical decision task in performance accuracy (but not response time). The results also revealed no relationship between lateralization in VWM and lexical decision. VWM performance accuracy decreased significantly with increasing asymmetry. This relationship was significant for women, but not men. Taken together, the present study demonstrates that the lateral bias in visual working memory is independent from language lateralization, and less lateralized individuals perform better than individuals with larger asymmetries in both visual half-field tasks.

Keywords: functional cerebral asymmetries; visual working memory; visual half-field paradigm; asymmetry–performance relationship; sex/gender



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1. Introduction

Working memory (WM) has been defined as the temporary maintenance of information for the performance of a task in the (near) future, including manipulation and updating of the information [1]. WM is an important element of many complex cognitive (language, visuospatial performance, etc.) and emotional processes, is related to intelligence [2,3], and is crucial for adequate functioning in a variety of situations such as learning, reading, and problem solving [1,4].

1.1. Visual Change Detection Task: Classical Version and Bilateral Modification

The visual change-detection task [5,6] is a well-established paradigm for investigating different aspects of visual working memory (VWM) [7–10]. In the visual change-detection task, participants are briefly (100–500 ms) presented with a memory array of visual objects (e.g., colored bars in various orientations, squares, other shapes), which is followed by a

short retention period (900–1000 ms) and a test probe. Participants are instructed to indicate whether the displayed test probe matches the previously viewed memory array or whether the probe has changed. One critical modification is the bilateral (or directional) version of the visual change-detection task [11]. This version of the task relies on the difference between an attended and non-attended side: the memory array is preceded by a centrally displayed arrow cue that points to the side of the screen from which participants encode visual stimuli that participants are asked to memorize, whereas they must ignore stimuli on the contralateral side.

The bilateral version of the change-detection VWM task allows to differentiate between ipsi- and contralateral visual pathways as stimuli presented to the right and left visual half-fields are dominantly processed by the left and right hemispheres, respectively. However, in the majority of studies using the bilateral change-detection task, contra- and ipsilateral brain responses and performance have been investigated without taking into account the visual half-field to which attention has been directed (e.g., [2,11–14]), and the studies that included visual half-field in the statistical design reported contradictory results [15–25]. Some of these studies reported faster and more accurate responses towards serially presented words in the RVF as compared to LVF, suggesting a RVF/LH advantage following lateralized encoding [18] and retrieval [19]. The lateralized color WM study [15] revealed LVH/RH advantage in accuracy for both encoding and retrieval. This advantage was most pronounced in a high compared to low memory load condition and was interpreted by the authors as RH superiority in encoding and retrieval of color stimuli when memory load is high, and a stronger LH involvement (i.e., reduced asymmetry) when memory load is low, probably due to a LH verbalization strategy when memorizing color stimuli. Notably, in this study, the LVF/RH advantage was found in 90% of men but only in 60% of women [15]. In an early psychophysical study [26], participants were asked to memorize either digits (verbal memory task) or digit positions (spatial memory task) presented for 80 ms in the right or left visual half-field. Similar to Clapp et al. [15], the results revealed visual half-field and sex/gender-specific findings: men recalled more digits (verbal memory) from the RVF than LVF, whereas women did not show any performance differences between visual half-fields. In addition, the recall of digit positions (i.e., spatial memory) did not differ as a function of the visual hemi-field despite the classical of a RH specialization for the spatial component of WM (e.g., [27,28]). More recent studies that administered the change detection task [16,17,21–23,25] did not find visual half-field differences in memory capacity, accuracy, or response time, but this might be partly due to the small sample sizes ($n \leq 16$), which caused small statistical power in these studies.

1.2. Stimuli in Change Detection VWM Studies

All change detection VWM studies mentioned above used shapes as stimuli. In fact, we found only one change detection VWM study [29] that used spatially organized letters to assess WM performance in parallel to ERPs recording. However, alphanumeric stimuli (letters and numbers) are frequently used in other WM paradigms such as the N-back task [30], serial order task [31], Sternberg task [32], and in the studies investigating the phonological loop (storage system in WM) [33]. However, letters are problematic as they can be memorized verbally or as simple visual stimuli (similar to shapes) [29]. If letters are stored in WM as verbal information, the RVF/LH advantage might simply indicate the well-known RVF/LH advantage for language processing [34]. For example, in an fMRI WM study, Axmacher et al. [35] demonstrated that verbal (but not spatial) WM processing mainly depends on language dominance, i.e., the regions that were engaged in language functions were also more involved in verbal WM processing. In other words, the LVF/RVF advantage in WM processing might be confounded by verbal/non-verbal (spatial) stimulus type and the hemispheric language specialization of participants.

To take stimulus type as potential confounder into account when investigating VWM, the present study therefore administered both (i) a VWM task with lateralized presentation of capital letters, and (ii) the translingual lexical decision task (TLDT, [36,37]). The

TLDT is an established visual half-field task for investigating the RVF/LH advantage in language lateralization [36,37]. The visual half-field technique is a simple, cost effective and well-established paradigm for investigating functional cerebral asymmetries in the visual domain (e.g., [38] for overview, but see also [34,39] for critical opinion). A large positive correlation of RVF/LH advantages in TLDT and VWM tasks would suggest a common left-lateralized processing mechanism for lexical decisions and letter storage in WM, and would supplement the idea that the laterality bias in letters processing in VWM depends on the language dominant hemisphere [35]. If, on the other hand, VHF advantages in both tasks were found to be unrelated, this would suggest that letters are stored and encoded as visual, not verbal stimuli. The results would also supplement previous findings of an ERP study, which found that the CDA (i.e., ERP component considered to be a load-dependent marker of VWM encoding and storage, [11]) was elicited by colored squares and letters, and its amplitude was load-dependent for both types of stimuli, suggesting usage of same neural mechanisms; that is, VWM in both tasks (instead of verbal WM for letters) [29].

1.3. Asymmetry–Performance Relationships

Brain lateralization has been found in human and non-human species, which leads many authors to conclude that it must be evolutionarily adaptive as it allows, for example, to perform multiple tasks simultaneously, avoids unnecessary duplications of functions, and increases processing speed due to reduction in interhemispheric communication (for reviews see [40–42]). In terms of cognitive performance, one can assume that larger functional cerebral asymmetries indicate more effective processing, and consequently better performance. However, results of studies investigating asymmetry–performance relationships in humans are inconsistent. Some studies revealed better performance in more lateralized participants [43–48], whereas others revealed the opposite [36,49–52]. Reasons why these inconsistencies occur are not fully understood. Factors contributing to these inconsistencies include variation between mental processes [53] and sensory modalities (e.g., [46,51]). For example, Boles et al. [53], aiming to evaluate asymmetry–performance relationships for different cognitive functions, assembled data from several studies that implemented visual half-field and dichotic listening tasks. The results demonstrated positive as well as negative asymmetry–performance relationships, which, according to the authors, depend on the age at which cerebral lateralization for different processes develop. The authors suggested that asymmetry–performance relationships are positive in early (auditory linguistic processing) and late (spatial positional processing) lateralizing processes, but negative for processes that reveal a laterality bias in the age between 5 and 11 years (e.g., spatial quantitative, visual lexical processing). In two independent studies, Hirnstein et al. [46,51] revealed U-shaped asymmetry–performance relationships that were negative for visually presented stimuli (word-matching and face-decision tasks) [51], but positive for dichotic listening [46]. In addition, individual differences, such as participants' age [44,46,48,54,55] and sex/gender [46,48,50,51,56] have been shown to affect brain lateralization, and therefore could be relevant in the context of the asymmetry–performance relationship. For example, Hirnstein et al. [51] evaluated asymmetry–performance relationships in word-matching and face-decision tasks and found that pronounced lateralization caused less accurate and slower performance in word matching task for both men and women. However, in a face-decision task, women with strong left-hemispheric biases performed slower but more accurately, contrary to men who demonstrated an inverted U-shaped asymmetry–performance relationship. Plessen et al. [48] demonstrated in a large ($n = 215$) MRI study that sex significantly moderated not just asymmetries in cortical thickness but also the correlations of cortical thickness asymmetry with vocabulary scores and verbal working memory. Specifically, they found that a positive relationship between cortical thickness (especially along the right mesial surface of the brain) and performance was stronger in men than women. Nevertheless, other studies failed to find substantial differences between men and women in asymmetry–performance relationships [36,46,50,56,57]. To the best

of our knowledge, there are no studies evaluating asymmetry–performance relationship for VWM.

1.4. Aims and Hypotheses of the Present Study

Taken together, there is conflicting evidence that does not allow to convincingly conclude that visual half-field differences in VWM exist. The assumption of an RVF advantage is almost entirely based on indirect evidence from the literature. It also remains unclear how potential laterality effects in VWM are related to performance and to what extent previous findings are confounded by interindividual differences such as participants' sex/gender. In addition, it is unclear whether letters stored in WM use verbal or visual WM resources. Therefore, the aims of the current study were (i) to evaluate behavioral right vs. left visual half-field asymmetry using a bilateral visual change-detection VWM task, (ii) to assess the relationship between asymmetries for lexical decision and VWM, (iii) to investigate relationship between VWM asymmetry and performance, and finally (iv) to determine to what extent sex/gender influences VWM lateralization in VWM per se and the lateralization–performance relationships.

It was hypothesized that an RVF/LH advantage would emerge for both the VWM and TLDT task, and that language asymmetry would correlate positively with VWM asymmetry if the latter is processed in verbal memory. On the other hand, if letters are stored as visual, not linguistic stimuli, then VWM and TLDT asymmetry indices will not correlate. We expected that assessment of the VWM performance in parallel to the evaluation of the language lateralization in a relatively large sample, involving both males and females, would reveal the potential effect of language lateralization on letters storage in WM.

2. Methods

2.1. Participants

We recruited 112 participants (21.79 ± 2.45 years, 68 women, 44 men) via personal contact and class advertisement in Vilnius University Life Sciences Center (see sub-section Demographic questionnaire for more details). Aiming to avoid possible effect of age- [13], medication-, and neural system-related disorders, general inclusion criteria were younger adult age (18–35 years), no history of head trauma or neuropsychiatric disorders, and not taking any medication affecting the CNS. Due to neuropsychiatric disorders (depression, panic disorder, epilepsy, head trauma) data of 8 participants were excluded; consequently, data of 61 women and 43 men were used for further analyses. All participants had normal or corrected to normal vision. All participants were White, as other ethnicities are still relatively rare in Lithuania.

The sample size was estimated using G*Power [58]. The a priori power analysis for ANCOVA test recommended a sample size of 96 participants to achieve a large effect size ($f = 0.4$; $\eta_p^2 = 0.14$) with an α value of 0.05, and power ($1 - \beta$ error probability) of 0.85.

Before the beginning of the experiment, participants signed the informed consent. The study was conducted in accordance with the guidelines of the declaration of Helsinki [59].

2.2. Demographic Questionnaire

Participants completed a self-reported questionnaire that assessed demographic information (age, sex, current health, and languages spoken). Although men (23.02 ± 2.48 years) were on average older than women (20.90 ± 2.04 years, $t(102) = 4.77$, $p < 0.0001$, Cohen's $d = 0.93$), this difference was numerically small (i.e., 2.12 years of age) and unlikely to be relevant for the present study. Moreover, age did not correlate significantly with any sex/gender-related parameters (i.e., memory capacity and asymmetry indices of performance, all $r \leq 0.11$, $p \geq 0.23$). Consequently, participants' ages were not included in further analyses. Ninety-nine participants were university students or had completed university with a BSc/MSc degree, 5 participants (2 women, 3 men) indicated having secondary education.

Although the impact of sex steroids was not the key focus of the present study, previous research indicated that sex hormones can affect functional brain asymmetries [30,60]. To rule out that the study sample was biased with respect to hormonal status of women, we added a self-reported questionnaire including questions about women's menstrual cycle and hormonal contraceptive use. According to the questionnaire, 63 women were naturally cycling and three were hormonal contraceptive users. Among naturally cycling women, 41 reported that their cycles were regular (mean duration 24–35 days) and provided information about their cycle day during the experiment. Based on the self-report, 15 were in the early follicular, 15 women were in the late follicular, 6 women in the mid-luteal and 5 women in the late luteal phase of their menstrual cycle. It should be noted that questionnaire data can only provide a rough estimate of women's cycle phase but suggests that female participants of the present study were heterogeneous in their hormonal status, and therefore it is unlikely that their behavioral data were hormonally biased.

2.3. Handedness

Participants' hand preference was estimated with the Lithuanian version of the Edinburgh handedness inventory [61]. The questionnaire consisted of 10 original activities suggested by Oldfield and the same response format as Oldfield's [61] original measure was used. Participants had to indicate the hand they prefer to use for each activity by putting a single cross in the left or right column. If the preference to use a particular hand was so strong that the participant would never use the other hand unless it is necessary, two crosses were to be put in the preferred column. The laterality index (LI) was calculated using the following formula: $LI = ((\text{sum of right-hand crosses} - \text{sum of left-hand crosses}) / (\text{sum of all crosses})) \times 100$. The scores of the LI ranged from -100 to 100 (mean $54.37 \pm SD 58.15$). Negative values indicated left-handed ($n = 13$) and positive values indicated right-handed preference ($n = 85$), one person scored zero, indicating no hand preference. The mean hand preference for men was (44.16 ± 65.13), and for women was (63.47 ± 50.39 , $t(102) = 1.70$, $p = 0.092$). Due to the numerical sex/gender differences in handedness, and similar to Hausmann et al. [36], handedness was used as covariate in the statistical design.

2.4. Language Lateralization

The current study adopted the well-established visual half-field task (i.e., translingual lexical decision task, TLDT, Figure 1A) and experimental design from two previous studies [36,37]. The TLDT was programmed in DMDX [62]. In each trial, two stimuli, either word(s) and/or non-word(s), were presented simultaneously to the right-visual field (RVF) and left-visual field (LVF). Sixteen lowercased words (agenda, alibi, aura, casino, film, gala, garage, jazz, jury, menu, radio, piano, snob, studio, taxi, virus) and 48 non-words were created using the pseudoword creator.

"Wuggy" [63] were used (see [36,37] for more details about word selection and [36] for the list of the word and non-word combinations). All stimuli were displayed in black Courier New font, lower case, size 12 on a computer screen with a white background. The stimulus eccentricity was between 2° and 5° of visual angle horizontally and 0.5° of visual angle vertically. Each trial started with a fixation cross presented for 1000 ms, followed by two word/non-word stimuli presented to the RVF and LVF for 100 ms. Participants had 2000 ms to decide and indicate by pressing a button on a keyboard, whether a meaningful word was presented to the LVF (left-sided button press with left index finger, "F" button), RVF (right-sided button press with right index finger, "J" button) or if there was no word on either side (by pressing the "space" button with the thumbs of both hands). If no answer was given, the next trial started.

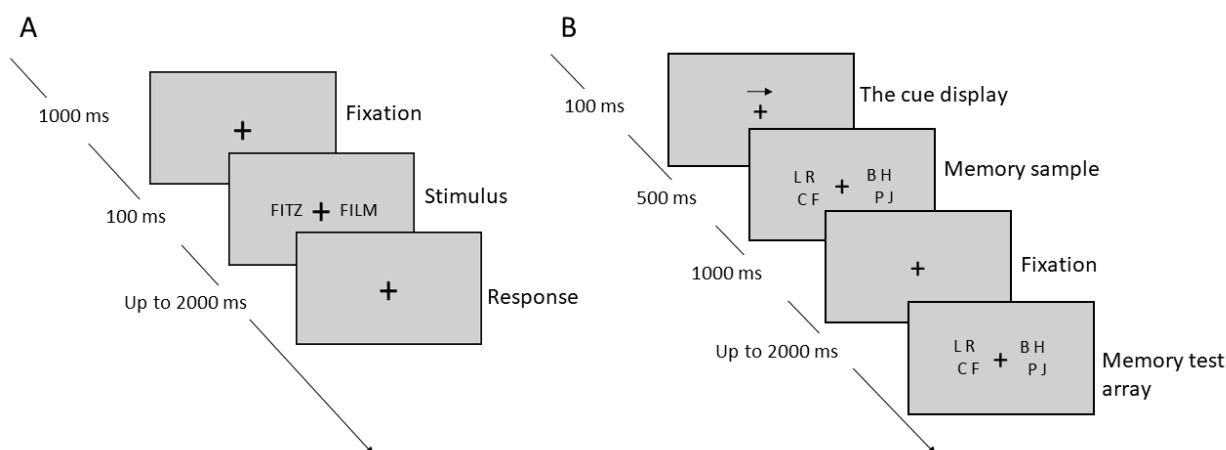


Figure 1. Schematic figures of: (A) the translanguagel lexical decision task (TLDT); (B) the visual working memory task (VWM).

In total, there were 256 trials; 64 trials when a meaningful word appeared in the LVF, 64 trials when a meaningful word appeared in the RVF, and 128 trials when no meaningful word appeared. After 128 trials participants took a self-paced break. Prior to the main experiment, participants performed 10 practice trials. The TLDT took approximately 20–30 min to complete.

For more detailed information on TLDT, see Hausmann et al. [36] and Willemin et al. [37].

2.5. VWM Task

The present study adopted the change detection paradigm [5,29] to measure visual working memory parameters (Figure 1B). All stimuli were presented in black Courier New font, in capital letters, on a gray (rgb 192; 192; 192) background. Participants were seated at an approximately 57 cm eye distance from the display, so that 1 cm corresponded to a 1° visual angle. Each trial started with a cue and a fixation cross presented for 100 ms. The cue was a black arrow (0.8° wide, 0.4° high) presented above a central fixation cross ($0.2^\circ \times 0.2^\circ$) and pointed to either the LVF or RVF. After the cue, a memory sample array was presented for 500 ms, based on previous VWM studies [13,29,55,64]. Two of these studies used letters as stimuli and presented these for 500 ms [29,55], and the other two demonstrated better performance in VWM task with a presentation time of 500 ms than with a presentation time of 100 ms [13,64]. Each memory sample array consisted of a fixation cross and bilateral sets of three, four or five capital letters C, E, M, P, S, T, V, and K (approx. 0.34° visual degree wide and 0.4° visual degree high). Letters were randomly arranged in the left and right visual half-fields within imaginary circles with a radius of 2° , 3.8° , 5.5° visual degrees. The stimuli eccentricity was 1.6° visual degree for inner and 4.3° visual degree for outer letters. Participants were instructed to memorize the letters in the cued visual half-field. After the memory sample array, a fixation cross appeared for 1000 ms and was followed by a memory test array. The memory test array was identical to the memory sample display in 50% of the trials. One letter, on the cued side, was changed relative to the corresponding memory sample in the remaining 50% of the trials. The positions of letters were balanced between RVFs and LVFs; changes were also distributed equally on both sides and with respect to the cross of fixation. The memory test display was presented for 2000 ms or until response. Participants were instructed to press 'F' with a left index finger, if the letter change was detected and 'J' with a right index finger, if no change was detected. If no response was given, the next trial started. The duration of intertrial intervals varied between 2100–2900 ms.

The task consisted of 240 trials (80 trials consisting of three-letter stimuli, 80 trials with four letters, and 80 trials with five letters in each visual half-field). After 120 trials, participants took a self-paced break. Ten practice trials were performed before the main

experiment. E-PRIME 2.0 software (Psychology Software Tools, USA) was used for stimuli presentation and data collection. The VWM task took approximately 30–35 min to complete.

2.6. General Procedure

The experiments were performed in a sound-proof and light-controlled room. All participants filled in the demographic and Edinburgh [61] questionnaires, received detailed tasks instructions. The TLDT was performed first, followed by approximately 15 min break and the VWM task. The whole session lasted approximately 90 min.

2.7. Data Analysis

The number of correct answers (ACC, %) and the response time of correct responses (RT, ms) were assessed for RVF and LVF. Sided and absolute asymmetry indices (AIs) were calculated. The scores of the sided AI take the direction of laterality bias into account and were calculated using formula: $[(RVF - LVF)/(RVF + LVF)] \times 100$. Sided AIs range from -100 to 100 . For clarity, AIs calculated from RT were inverted so that positive values always indicated RVF/LH advantage. Absolute AIs were calculated as absolute value of sided AIs and showed asymmetry magnitude, irrespective of whether the laterality bias was to the left or right, resulting in values between 0 and 100 [36]. Smaller AIs around 0 indicate less asymmetries whereas larger AIs around 100 indicate pronounced asymmetries.

Similar to Hausmann et al. (2019), we excluded data of participants based on individual VWM task performance by calculating thresholds above/below chance based on binomial tests [65]. Before exclusion there were 104 participants (63 women, 41 men). The number of trials for one visual half-field was 120. Accordingly, the number of 72 correctly identified targets (60%) was used as an upper threshold (for the visual half-field with the higher performance) and 48 correctly identified targets (40%) was used as a lower threshold (for the visual half-field with the lower performance). Eighty-two participants demonstrated RVF advantage, twenty LVF advantage and two performed equally for RVF vs. LVF. Data of five (all with RVF advantage) participants were excluded because performance for stimuli presented in their dominant VHF was not significantly above chance level. Consequently, data of 99 participants (59 women, 40 men) were analyzed.

For the main analyses, mixed ANCOVA and Bonferroni test were used for post hoc. The sphericity assumption for repeated measures was tested with Mauchly's test. If sphericity assumption was violated, Greenhouse–Geisser correction was applied.

Pearson correlation analyses were performed to evaluate the relationships between performance parameters from VWM and TLDT. For relations between lateralization and performance, both linear and quadratic (only for sided AIs) regressions were calculated, as previous studies suggested U-shaped relationship between the degree of lateralization and performance when sided AIs were considered [51,53].

Data were analyzed using IBM SPSS20. This study's design and its analysis were not pre-registered.

3. Results

3.1. VWM Performance Accuracy

The performance accuracy was calculated using a formula: performance accuracy (%), $ACC = (((p(\text{hit}) + p(\text{correct rejection}))/2) - p(\text{false alarm})) \times 100$, where: $p(\text{hit}) = \text{hit number}/20$; $p(\text{false alarm}) = \text{false alarm number}/20$; $p(\text{correct rejection}) = \text{correct rejection}/20$; 20 —number of trials per condition.

ACC of the VWM task was subjected to a 2 (LVF vs. RVF) $\times 3$ (three vs. four vs. five letters) $\times 2$ (male vs. female) mixed ANCOVA. Handedness and AIs calculated from accuracy in TLDT were included as covariates. The analysis revealed significant RVF advantage, $F(1, 94) = 38.59$, $p < 0.0001$, $\eta_p^2 = 0.29$, indicating more accurate performance when stimuli were presented in the RVF ($76.3 \pm 10.3\%$, $M \pm SD$) as compared to LVF ($67.9 \pm 11.9\%$). The effect of the number of letters that participants needed to remember was significant too, $F(2, 188) = 157.47$, $p < 0.0001$, $\eta_p^2 = 0.63$. As expected, performance

accuracy decreased with increasing number of stimuli (all $p < 0.0001$) (Figure 2). *Post hoc* tests revealed the significant RVF advantage in all three VWM conditions (RVF: three letters: 91.5 ± 8.1 %, four: 77.8 ± 14.2 %, five: 59.7 ± 17.5 %; LVF: three letters: 84.1 ± 11.2 %, four: 67.2 ± 17.6 %, five: 52.5 ± 17.6 %, all $p < 0.05$ (Figure 2)). No other main effect or interaction approached significance, all $F \leq 2.2$, $p \geq 0.113$.

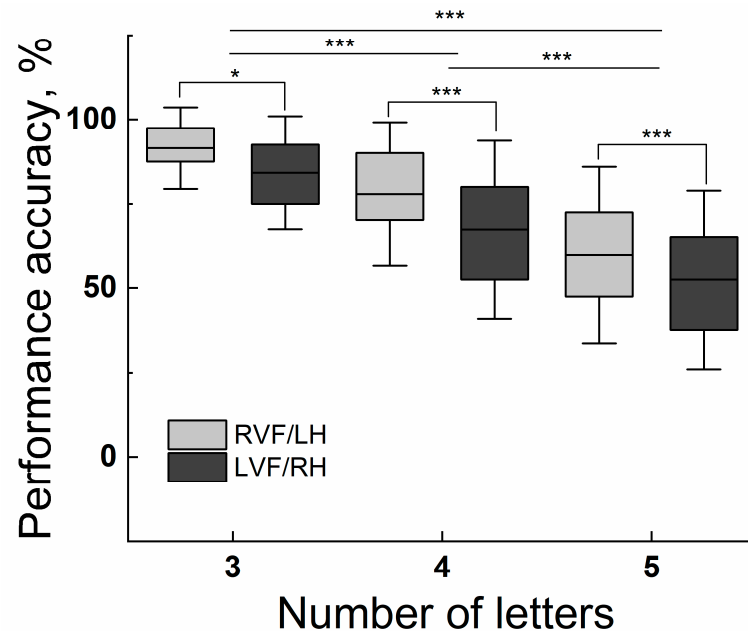


Figure 2. Mean and standard deviations of performance accuracy in three, stimuli set sizes related, conditions of the VWM task. * $p < 0.05$, *** $p < 0.0001$.

3.2. VWM Response Time

RT (ms) of correct responses of the VWM task was subjected to the same mixed ANCOVA as used for ACC. Handedness and AIs calculated from RT in TLDT were included as covariates. In line with performance accuracy, the analysis revealed significant RVF advantage; $F(1, 94) = 14.17$, $p < 0.0001$, $\eta^2_p = 0.14$, i.e., faster responses to stimuli presented in RVF (887 ± 156 ms) as compared to LVF (916 ± 161 ms). Moreover, the effect of the condition (number of letters) was significant, $F(1.33, 124.9) = 90.40$, $p < 0.0001$, $\eta^2_p = 0.49$. As expected, the more letters participants needed to remember, the longer response time was, and all conditions differed significantly from each other: stimuli presented in RVF: three letters: 807 ± 158 ms, four – 902 ± 163 ms, five: 950 ± 171 ms; in LVF: three letters: 843 ± 164 ms, four: 931 ± 167 ms, five: 972 ± 174 ms (all $p < 0.0001$, Figure 3). The analysis also revealed tendency of interaction between the visual half-field and number of letters: $F(1.99, 124.9) = 2.42$, $p = 0.092$, $\eta^2_p = 0.03$. *Post hoc* showed that difference between visual half-fields decreased with increase in memory load (three stimuli $t(98) = -6.58$, $p < 0.0001$; four stimuli $t(98) = -4.07$, $p < 0.0001$; five stimuli $t(98) = -2.76$, $p = 0.007$). No other main effect or interaction approached significance, all $F \leq 2.42$, $p \geq 0.092$.

3.3. VWM Capacity

Following formula was used for working memory capacity calculation: memory capacity = $((p(\text{hit}) - p(\text{false alarm})) / (1 - p(\text{false alarm}))) \times \text{set size}$, where: $p(\text{hit}) = \text{hit number} / 20$; $p(\text{false alarm}) = \text{false alarm number} / 20$; 20—number of trials per condition [10]. The memory capacity can potentially range between 0 and 5, indicating a number of stimuli participant can maintain in VWM.

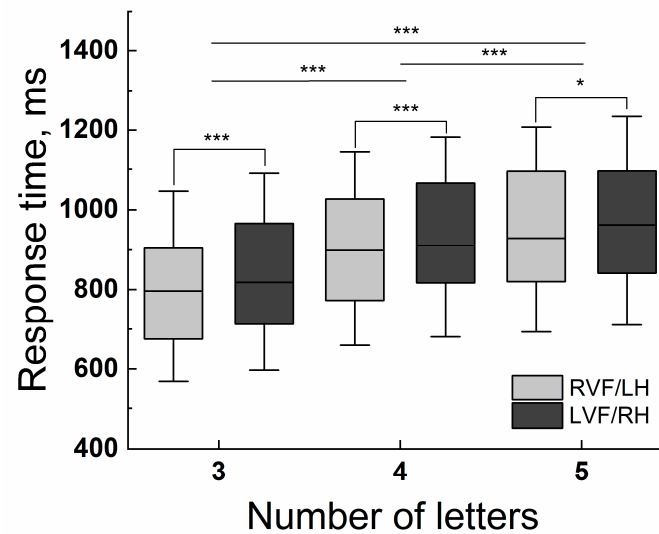


Figure 3. Mean and standard deviations of response time in three, stimuli set size related, conditions of the VWM task. * $p < 0.05$, *** $p < 0.0001$.

Memory capacity was subjected to a 2 (LVF vs. RVF) \times 2 (male vs. female) mixed ANCOVA with handedness and AIs calculated from ACC in TLDT as covariates. The ANCOVA revealed the significant visual half-field effect; $F(1, 94) = 6.02$, $p = 0.016$, $\eta^2_p = 0.06$, indicating higher memory capacity when stimuli were presented in the RVF (3.05 ± 0.50) as compared to LVF (2.93 ± 0.53). Moreover, there was a significant interaction between sex and visual half-field; $F(1, 94) = 4.43$, $p = 0.038$, $\eta^2_p = 0.05$. *Post hoc* t-tests revealed that women's memory capacity was higher when words were presented in the RVF (3.1 ± 0.49) than in the LVF (2.87 ± 0.56 , $t(58) = 3.96$, $p < 0.0001$), while men's memory capacity did not differ between visual half-fields (RVF 3.01 ± 0.52 , LVF 3.01 ± 0.48 , $t(39) = -0.06$, $p = 0.96$) (Figure 4). All other main effects and interactions did not approach significance, all $F \leq 1.50$, $p \geq 0.22$.

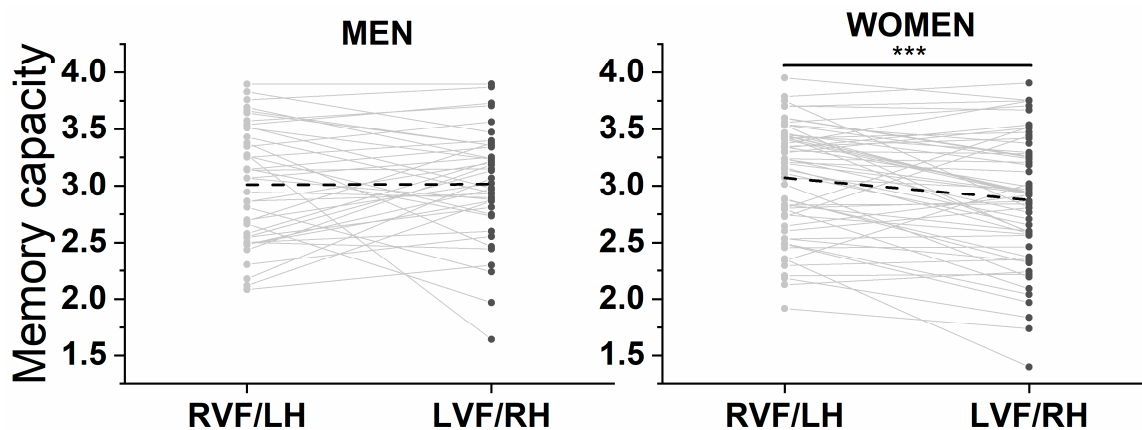


Figure 4. Men's and women's memory capacity (means (in black dotted line) and participant values (in grey)) for right (RVF) vs. left (LVF) visual half-field. *** $p < 0.001$.

3.4. VWM Asymmetry Indices

Frequency analysis revealed that 81% participants showed RVF advantage (positive-sided AI values) for performance accuracy ($X^2(1, 99) = 39.23$, $p < 0.0001$), 71% for RT ($X^2(1, 99) = 18.68$, $p < 0.0001$) and only 56% for memory capacity ($X^2(1, 99) = 1.22$, $p = 0.27$) (Figure 5). These results are in line with the ANOVA and indicated that mean AIs, showing better performance in RVF condition, were not simply based on outliers.

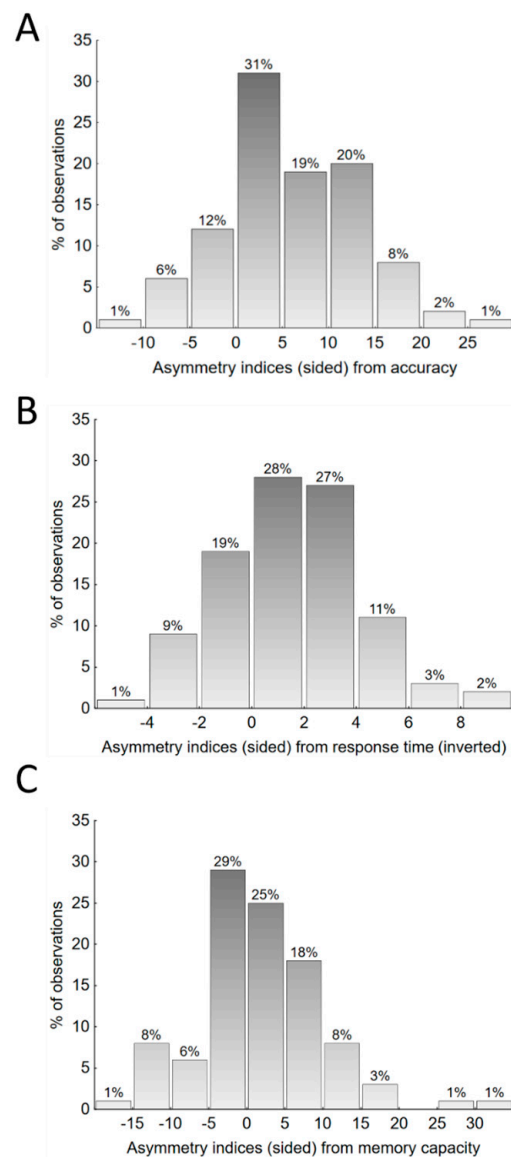


Figure 5. Distribution of the sided (directional) asymmetry indices (AI_{sd}) calculated from: (A) performance accuracy, (B) response time (inverted), and (C) memory capacity.

3.5. TLDT Performance

In line with the previous TLDT studies [36,37], there was significant RVF/LH advantage $F(1, 88) = 6.52, p = 0.01, \eta^2_p = 0.07$ in ACC. ACC was higher ($\Delta = 8.7\%$) when words were presented to the RVF/LH (61.7 ± 13.9) than to the LVF/RH (53.0 ± 14.3). Nevertheless, it is worth noticing that the effect of visual half-field on ACC was much smaller in the present study than in both previous ($\eta^2_p = 0.44$ [37] and $\eta^2_p = 0.26$ [36]). Moreover, in contrast to the same previous studies [36,37], the visual half-field effect did not occur for RTs ($F(1, 88) = 1.01, p = 0.317$) in the present study (RT: RVF/LH 692 ± 129 , LVF/RH 712 ± 109). Sex/gender has no significant effect on ACC or RT (all $p \leq 0.15$). Moreover, in line with previous studies [36,37], the visual half-field effect did not interact significantly with sex/gender.

3.6. Relationship between TLDT and VWM Performance

Pearson correlation analysis, performed to evaluate relationships between TLDT AI and VWM AI, did not show relationship between sided AI of two tasks ($r(89) = 0.02, p = 0.82$) (Figure 6). In addition, the VWM AI was calculated separately for three, four,

and five letter conditions and correlated with TLDT AI but did not reveal significant relationships (respectively: $r(89) = -0.05$, $p = 0.61$, $r(89) = 0.18$, $p = 0.09$, $r(89) = -0.08$, $p = 0.48$).

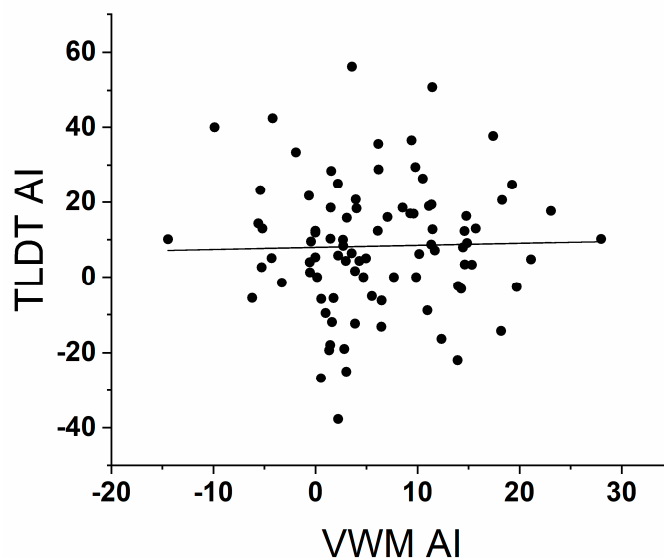


Figure 6. Relationship between the sided (directional) asymmetry indices (AI) of VWM and TLDT tasks.

3.7. VWM Performance Comparison between Participants with Typical and Atypical TLDT Asymmetry

Several previous studies [35,47] presented an interesting idea about the effect of typical (left) vs. atypical (right) language dominance on other cognitive functions, including WM. The present study aimed to investigate the idea that language lateralization (as assessed by TLDT) might impact on the VWM of letters more directly by comparing VWM performance of participants with typical (left dominant) and atypical (non-left dominant) language lateralization. The analysis of asymmetry indices calculated for TLDT revealed that 63 (69.2%) participants demonstrated typical (RVF/LH) advantage, 24 (26.4%) participants demonstrated atypical (LVF/RH) advantage, and 4 (4.4%) showed no laterality bias in TLDT accuracy. From a subgroup of typical language lateralization, 24 participants were selected to match the 24 participants with atypical language lateralization as measured with TLDT. However, simple comparisons between both groups did not reveal any significant differences in VWM accuracy, response times or AIs between these two groups (all $t \leq 1.7$, $p \geq 0.1$).

3.8. Asymmetry–Performance Relationships in VWM

The present study investigated asymmetry–performance relationships for the whole sample and for women and men separately. The evaluation of sex/gender effect was encouraged by studies showing sex/gender differences in asymmetry–performance relationships [48,51]. Regression analyses (linear and quadratic) were performed for both sided and absolute AIs, with mean ACC, RT, and memory capacity (both collapsed for RVF and LVF) (Table 1). The regression analyses revealed that correlation coefficients were consistently negative across all measures (although not all correlations were statistically significant), indicating that larger asymmetries in VWM were related to lower VWM performance. The correlation coefficients were even larger for quadratic regression, which might indicate optimum performance when VWM asymmetry was rather small. This effect was only significant in women, not men.

Table 1. The linear and quadratic regressions between sided and absolute asymmetry indices (AIs) and overall (collapsed for LVF and RVF) VWM performance accuracy, response time, and memory capacity for all participants and across both sexes. Significant relationships ($p \leq 0.01$, after correction for multiple comparisons) are shown in bold. Negative r values in quadratic regressions indicate inverted U-shape relationships. Optimal AI indicate which AIs were associated with optimal performance.

	Accuracy r (Optimal AI)	Memory Capacity r (Optimal AI)	Response Time r (Optimal AI)
Sided (directional)AIs			
Linear regression			
All participants	−0.29 **	−0.17 #	0.005
Women	−0.40 **	−0.26 #	0.004
Men	−0.13	−0.06	0.027
Quadratic regression			
All participants	−0.41 (1.61) ***	−0.25 (1.82) *	−0.13 (−1.09)
Women	−0.51 (2.36) ***	−0.26 (−6.67)	−0.18 (−2.55)
Men	−0.29 (2.38)	−0.28 (4.88)	−0.07 (−1.09)
Absolute AIs			
Linear regression			
All participants	−0.39 ***	−0.25 **	−0.10
Women	−0.49 ***	−0.29 *	−0.12
Men	−0.21	−0.20	−0.07

Note: AIs—asymmetry indices, #— $p \leq 0.1$, *— $p \leq 0.05$, **— $p \leq 0.01$, ***— $p \leq 0.001$.

4. Discussion

The results of our study showed an overall RVF advantage in a bilateral change-detection WM task with letters as stimuli, suggesting a dominance of the language-dominant left hemisphere in VWM. The RVF advantage was independent of participant's sex/gender as well as handedness. Moreover, language lateralization as determined by TLDT was not related to VWM performance. In addition, smaller VWM asymmetry was related to more accurate VWM performance and higher memory capacity.

The RVF advantage in VWM is in agreement with other studies showing an RVF advantage for digit recall [26] and word processing [18,19]. It is also important to note that single letters have previously been shown to produce a secure RVF advantage in VHF tasks [66]. However, it is unlikely that the RVF advantage is simply due to the verbal nature of the task and the well-known left hemisphere's dominance in processing verbal information [34,36,37] because the lexical decision asymmetry, determined by TLDT, was not related to VWM performance. Moreover, we did not find differences between participants showing typical (RVF/LH) and atypical (LVF/RH) language lateralization, as determined by TLDT, in VWM accuracy, response times, and asymmetry indices. This indicates that participants who showed larger RVF/LH advantage in lexical decision task were not necessarily the same participants who were more lateralized in the same direction in the VWM task. The findings of the previous electrophysiological WM study [29] showed that letters, despite their verbal associations, elicited the visual (not verbal) working memory-related ERP component. Similarly, the missing relationship between performance asymmetry in VWM and TLDT asymmetry in the present study suggests that letters were maintained/processed in visual, but not verbal working memory. In a fMRI study of visual memory, Sheremata et al. [23] showed that during VWM processing left hemisphere IPS was strongly biased for contralateral targets, but right hemisphere IPS exhibited effects for stimuli placed in both visual half-fields. Moreover, Mesulam [67] proposed the model of hemispheric specialization of visuospatial attention, which is an integral part of VWM

(see e.g., [68,69]), suggesting that the LH is concerned almost exclusively with attention to the contralateral right hemifield, whereas the RH is capable of directing attention to both sides of space. Therefore, stimuli from RVF could be processed in VWM more efficiently because of projections to contra- as well as ipsilateral hemispheres.

Nevertheless, the RVF advantage in the presented study could potentially be explained by the left-to-right reading habit in our sample. It has been demonstrated that the higher resolution of perception and the allocation of visual attention in the RVF in skilled left-to-right readers [70,71] is absent in Hebrew (right-to-left) and bilingual readers [70] and in subjects with disturbed reading [71]. Therefore, the effect of habitual reading direction on visual perception and VWM cannot be fully ruled out.

4.1. Asymmetry–Performance Relationships

The investigation of asymmetry–performance relationship revealed a significant negative correlation between asymmetry indices and VWM task performance. The negative correlation was strongest between asymmetry indices and performance accuracy and was best described by an inverted U-shape curve (quadratic regression), i.e., the accuracy was lower when asymmetries were larger. The relationship between asymmetry indices and memory capacity or response time was weaker and mostly not significant but indicated the same direction interaction—lower asymmetry was related to faster responses and higher memory capacity. To the best of our knowledge there are no previous studies evaluating the asymmetry–performance relationship in a change detection VWM task. Nevertheless, our results are consistent with those showing a negative relationship between the degrees of lateralization and performance on various verbal tasks involving semantic language decision, vocabulary and verbal fluency [49], remembering of words [50], translingual decisions [36], and word-matching [51]. However, there are also data showing opposite direction asymmetry–performance relationships across different cognitive functions, e.g., better reading performance [43], higher verbal IQ scores, better visuospatial skills [44,45], and higher accuracy in a dichotic listening task [46] in more lateralized participants. Thus, it seems that the asymmetry–performance relationship could be both negative and positive and depends on methodological aspects (cognitive functions, tasks, methods of lateralization determination, etc.) as well as individual characteristics (age, handedness, sex, etc.).

4.2. Sex Effect

In line with previous studies (e.g., [36,72,73]), no consistent sex/gender difference in the degree of performance lateralization was found, with one exception—women's, but not men's memory capacity was higher when words were presented in the RVF than in the LVF. Absence of the sex/gender difference was opposite to two previous studies showing the small effect of interaction between sex and visual half-field in a word-matching task (RVF advantage in women, but not men) [51] and in a digits recall task (RVF advantage in men but not women) [26]. In the present study and in both previous studies, the sex/gender effect on performance lateralization was small and should be interpreted with caution. Nevertheless, the results of present study also revealed the sex/gender effect in asymmetry–performance analysis. Here, the negative relationship between asymmetry and performance occurring in a whole sample became even stronger when evaluated in women and much weaker and non-significant when evaluated in men. It could be that this is an accidental finding and lower correlation in the male group may be simply explained by the lower men number in our sample. Nevertheless, it is interesting that in a word-matching study [51] (where there were also fewer men than women), negative correlation between asymmetry and performance accuracy was also lower in men as compared to women. It has been suggested that the asymmetry–performance relationship might depend on cooperation between the hemispheres via corpus callosum [72,74]. Therefore, the microstructural organizational differences of the corpus callosum between men and women [75] might, at least partly,

explain not only sex/gender differences in functional brain asymmetries [60,76], but also the slightly different asymmetry–performance relationship.

4.3. Limitations

There are a few methodological aspects that are important to consider when interpreting the results of the present study. First of all, this refers to the relatively long stimuli presentation time (500 ms), which is longer than the tachistoscopic stimulus presentation of 150–500 ms typical in VHF studies. However, the longer presentation time in VWM tasks is needed to ensure that the performance is above chance level [13,64], and 500 ms presentations were used in the only previous VWM change detection study that also used letters as stimuli and demonstrated that letters are stored visually but not verbally in WM [29]. Furthermore, the laterality bias has been demonstrated in studies where presentation times are several seconds long such as the emotional chimeric faces tasks and the greyscales task [77–79]. Nevertheless, future studies should use shorter stimulus presentations or control for eye movement with eye-tracking devices for visual half-field presentations longer than 200 ms. Second, the response format of the TLDT in the present study was identical to two previous studies [36,37], which used three manual response (i.e., left hand response for targets in the LVF, right hand response for targets in the RVF, and bimanual response when no target was presented). For consistency, the same response format was applied for the VWM change detection task with the only difference being that no bimanual response was required, which bares the risk of manual stimulus–response compatibility effects. However, we consider this risk to be relatively small as (a) no compatibility effects were found when piloting the tasks, and (b) the present study included left- and right-handers and no handedness effects were found. Third, laterality has been shown to be sex/gender sensitive [60,76,80] and although sex/gender differences were not in the focus of the present study, sex/gender of participants was recorded and included in the statistical analyses. Although sex/gender could have been better balanced across participants, the current results suggest that a much larger sample size would have been necessary to find significant sex/gender differences. Moreover, previous studies suggested that an appropriate analyses of sex/gender differences would require an analysis of participants' hormonal status (e.g., [81–85]). Forth, the evidence of a non-existing correlation between TLDT and VWM performance should be taken with caution; a lack of association between two tasks could be partly confounded by low test-retest reliability of the tasks in this sample [86], as previous laterality studies have shown dynamic fluctuations in laterality patters due to, for example, fluctuations in mood and sex (e.g., [60,87]). Finally, the participants of the current study were white younger adults, with most of them being university students living in Lithuania. Therefore, absence of full demographic data regarding age, race/ethnicity, and socioeconomic status may limit generalizability.

5. Conclusions

In summary, the current study is one of the few studies using letters as stimuli in a lateralized change-detection VWM task. The results of the present study suggest RVF bias in VWM, which is independent of sex, handedness, and language processing. In addition, and to the best of our knowledge, this is the first study showing the negative asymmetry–performance relationship in visual WM. However, a deeper understanding of at which stage of the VWM process lateralization emerges would require a separation of the entire VWM process into sensory, cognitive (attention, memory encoding, and retrieval related) and motor subprocesses; for example, with ERP.

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