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A horizontal–vertical anisotropy in spatial short-term memory

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ABSTRACT
Visual perception and saccadic eye-movements are more precise when directed at isoeccentric locations along the horizontal compared to vertical meridian. This effect is known as horizontal-vertical anisotropy (HVA). Given that the eye-movement system plays an important role in spatial short-term memory (STM) it was hypothesized that spatial STM would also show a horizontal-vertical anisotropy. Consistent with this hypothesis an online experiment revealed a significant HVA in spatial STM (Experiment 1). This effect persisted even when eye-movements were precluded by using very short display durations (Experiment 2). However, there was no HVA in a colour span or orientation change detection task. It is argued that the HVA in spatial STM may result from greater imprecision in the representation of spatial locations along the vertical meridian relative to the horizontal meridian in the spatial maps underpinning spatial STM, a bilateral field advantage, or some combination of these mechanisms.

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Visual perception is not homogenous across the visual field. One notable example of this inhomogeneity is the horizontal–vertical anisotropy (HVA), which refers to the observation that visual perception of stimuli at isoeccentric locations is better along the horizontal meridian than the vertical meridian (Pointer & Hess, 1989). This perceptual HVA can be observed in many dimensions, including letter identification (Mackeben, 1999), orientation discrimination at eccentricities of 10 degrees or greater (Barbot et al., 2021; Rovamo et al., 1982), spatial frequency discrimination (Carrasco et al., 2001), contrast sensitivity (Abrams et al., 2012; Baldwin et al., 2012; Pointer & Hess, 1989; Rijsdijk et al., 1980), spatial crowding (Greenwood et al., 2017; Petrov & Meleshkevich, 2011) and spatial localization (Greenwood et al., 2017). The perceptual HVA cannot be explained in terms of anisotropic allocation of attention (Carrasco et al., 2001) and has instead been attributed to low-level physiological differences in the visual system such as reduced densities of ganglion cells and sparser cone density with increasing eccentricity along the vertical compared to the horizontal midlines (Carrasco et al., 2001).

A similar HVA exists in the oculomotor system, such that saccades with amplitudes of 5 degrees or more executed along the horizontal plane have shorter latencies, higher peak velocities and better accuracy compared to saccades directed to isoeccentric locations along the vertical plane (Bhidayasiri et al., 2001; Greenwood et al., 2017; Irving & Lillakas, 2019). Bonnett et al. (2013) argued that these effects become more pronounced with increasing age, although not all studies have been able to replicate this effect (Irving & Lillakas, 2019). Vertical saccades are also more vulnerable to distractor interference, displaying larger curvature effects than saccades along the horizontal plane (Laidlaw & Kingstone, 2010; Van der Stigchel & Theeuwes, 2008; Walker et al., 2006) and visual scanning is more efficient along the horizontal axis than the vertical axis, such that saccades are larger and fixations durations shorter (Phillips & Edelman, 2008).

The cause of the oculomotor HVA is not clear. One possibility is that it derives from the perceptual HVA, such that visual inputs from more superior and inferior locations along the vertical meridian generate weaker activation in the salience maps that drive eye-

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movements than isoeccentric locations along the horizontal meridian (Greenwood et al., 2017; Irving & Lillakas, 2019). Alternatively, they may reflect some neuroanatomical constraints on the oculomotor system. The horizontal and vertical components of saccades are generated by separate structures in the brainstem (respectively the parapontine reticular formation, PPRF, and the rostral interstitial nucleus of the MLF, RIMLF) and the distribution of burst neurons is more sparse in the RIMLF than the PPRF (Büttner-Ennever, 2008). Saccade metrics such as peak velocity and amplitude are derived from the activity of these burst neurons, so these structural differences are a plausible source of the HVA in eye-movements (Irving & Lillakas, 2019). A third possibility proposed by Foulsham and colleagues (Foulsham et al., 2008) is that the asymmetry is functional, arising due to the greater utility of horizontal compared to vertical saccades in visual exploration.

The existence of a HVA in the visual and oculomotor systems may have implications for cognitive processes that are known to be tightly coupled with the oculomotor system such as spatial attention (Awh et al., 2006; Casteau & Smith, 2019; Smith et al., 2021; Smith & Schenk, 2012) and visuo-spatial short-term memory (Ikkai & Curtis, 2011; Lawrence et al., 2004; Pearson et al., 2014; Pearson & Sahraie, 2003; Peterson et al., 2019; Postle et al., 2006; Smith & Archibald, 2020; van Ede et al., 2019), see also Heuer et al. (2020); Olivers and Roelfsema (2020) for recent reviews. Indeed, there is some evidence that the HVA is preserved in visual short-term memory. For example, Montaser-Kouhsari and Carrasco (2009) asked five participants to perform a match to sample task in which participants memorized a centrally presented standard (7 c/d gabor), then judged whether a briefly presented stimuli appearing 6 degrees into the periphery along the horizontal or vertical midlines were of a higher or lower spatial frequency. Performance was significantly better when test stimuli were presented along the horizonal compared to vertical meridians. The authors attribute this effect to decreased precision in encoding of the test stimulus that appeared on the vertical meridian.

In contrast to visual short-term memory, no studies have examined the extent to which the HVA is preserved in spatial short-term memory (STM). Given the key role the oculomotor system plays in visuospatial STM it seems reasonable to predict that anisotropies in the oculomotor system might produce a HVA in spatial STM. This prediction was tested in two experiments. Experiment 1 measured spatial memory using a variant of the Corsi blocks task previously used to measure spatial STM along the horizontal and vertical meridians in patients with Progressive Supranuclear Palsy (Smith et al., 2021; Smith & Archibald, 2020). Visual STM was measured with a task that required participants to recall sequences of colours presented along the horizontal and vertical meridians. In Experiment 2 a full report change detection task was used to assess memory capacity (k). In the spatial memory condition one of the stimuli changed location, in the visual memory condition one of the stimuli changed orientation. It was predicted that visuospatial STM span (Experiment 1) and visuospatial STM capacity (Experiment 2) would be significantly shorter for the vertically aligned stimuli compared to the horizontally aligned stimuli.

Experiment 1

Methods

Participants

196 participants were recruited through the Dept of Psychology Participant pool and social media, of whom 106 completed the spatial memory task (8 male, 97 female and 1 non-binary; median age 20 years) and 90 completed the colour memory task (24 males, 63 females, 2 did not state a gender, 1 non-binary; median age 21.01 years). People who took part via the participant pool were awarded pool credit. No compensation was offered to other participants. All participants gave informed consent via an online consent form. The study was approved by Durham University Dept. of Psychology Research Ethics Committee (PSYCH-2021-04-08T13:13:08-dps1ds).

Stimuli and apparatus

Participants completed the experiment on their own personal computer or laptop. Experimental stimuli were generated using PsychoPy3 (Peirce et al., 2019) and data were collected online using Pavlovia. As the size of stimuli varied depending on the specifications of participant's computers and their distance from the screen, dimensions are provided in pixels.

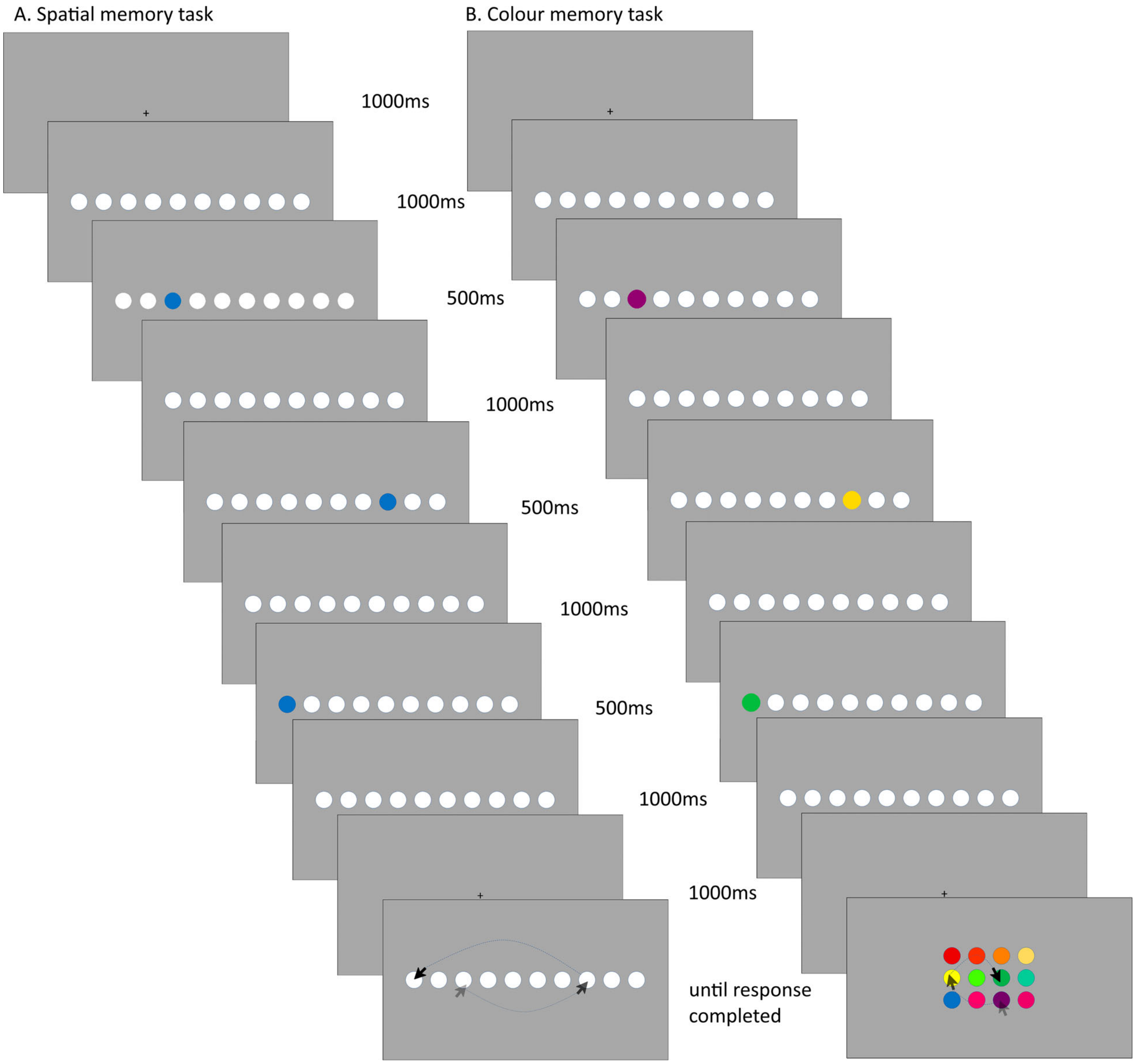

Figure 1. Illustration of the experimental procedure in Experiment 1.

The fixation point was as white cross (20 × 20) presented at the centre of the screen. In both tasks, the memory array comprised 10 white discs (40 × 40) aligned along either the horizontal or vertical midline, such that 5 discs fell in each hemifield. The centres of adjacent discs were separated by 80 pixels. In the spatial task, the to-be-remembered locations were indicated by the appearance of a blue disc (40 × 40). In the colour memory task, the memory items were 40 × 40 coloured discs. The colours were drawn from the following HTML colour set: Crimson, OrangeRed, Orange, Gold, Yellow, YellowGreen, Green, CadetBlue, Blue, Magenta, Purple, MediumVioletRed.

Procedure

Spatial Task: Trials began with the appearance of the fixation point for 1000 ms, followed by the onset of the memory array. After 1000 ms the sequence of memory items began, starting with 2 items. Each item in the sequence appeared for 500 ms and there was 1000 ms between items. 500 ms after the final item had been presented the array was replaced with a fixation cross for 1000 ms. The array then re-appeared and the participant was required to click on the correct sequence of locations using the mouse (see Figure 1(a)) Participants were given feedback on whether they had got the sequence correct.

Colour task: Trials began with the appearance of the fixation point for 1000 ms, followed by the onset of the memory array. After 1000 ms the sequence of memory items began, starting with 2 items. Each item in the sequence appeared for 500 ms and there was 1000 ms between items. 500 ms after the final item had been presented the array was replaced with a fixation cross for 1000 ms. A 3 × 4 array of coloured spots appeared and participants were required to click on the colours in the sequence they had been presented. Figure 1(b) illustrates this procedure.

Participants had to recall 3 sequences for each span length. If participants got 2 out of 3 sequences correct the span length was increased by 1 item and they were presented with 3 more trials. If they got 2/3 incorrect the trial terminated and the next trial began, starting with a span of 2 items. The maximum span length was 10 items. Participants completed 3 horizontal trials and 3 vertical trials. Horizontal and vertical blocks were interleaved, starting with horizontal.

Results

Data were analysed with a 2 (Orientation) × 2 (Task) mixed ANOVA. There were significant main effects of Task ($F_{(1,194)} = 130$, $p < .001$, $\eta^2p = .4$) and Orientation, ($F_{(1,194)} = 4.75$, $p = .03$, $\eta^2p = .023$), and a significant Task x Orientation interaction $F_{(1,194)} = 6.47$, $p = .012$, $\eta^2p = 0.032$, representing a small effect size. Post-hoc tests indicated a significant difference between the horizontal and vertical conditions in the spatial memory task ($M_{hor} = 4.51$, SD = 1.14; $M_{ver} = 4.22$, SD = 1.27; $F = 10.72$, $p = .001$) such that memory spans along the horizontal axis were significantly longer compared to memory spans along the vertical axis. There was no significant difference between the horizontal and vertical conditions in the colour memory task ($M_{hor} = 2.67$, SD = .94; $M_{ver} = 2.69$, SD = 1.27; $F = .07$ $p = .79$). Figure 2 illustrates these effects.

Discussion

This experiment tested the hypothesis that the HVA in perception and oculomotor control would be inherited by visuospatial short-term memory. Consistent with this hypothesis, there was a small but significant HVA on the Corsi task, such that memory spans were longer when stimuli were presented along the horizontal axis compared to the vertical axis. However, no HVA was observed for the colour memory task.

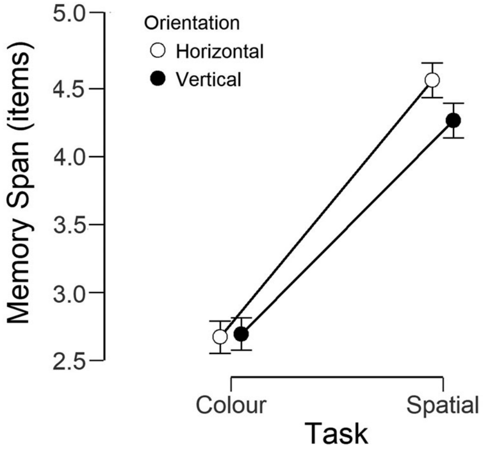

Figure 2. Memory spans in for colours and spatial locations presented along the horizontal and vertical meridians. Error bars show 95% confidence intervals.

The perceptual HVA is typically measured with the eyes fixated in the centre of the screen, so as not to confound the encoding of peripheral stimuli with a saccadic eye movement that would permit the participant to foveate the stimulus. However, in the current task eye-movements were not constrained so participants may have made eye-movements to fixate the locations of the memoranda. This would be particularly adaptive for the colour memory task, given that colour perception rapidly declines with eccentricity from the fovea. In this case, any effect of a perceptual HVA on memory would be compensated for by the fact that the stimuli were foveated. Performance on the colour memory task was also considerably worse than that on the spatial memory task. This may be because the memoranda in the colour task were much more similar to one another than the locations in the spatial task. The rationale was to reduce the probability of verbal encoding, but an unforeseen consequence appears to have been to make the colour stimuli more easily confused.

Given these confounds it seems premature to draw any conclusions about the existence of a HVA for visual STM. A solution to the issue of eye-movements is to enforce fixation during the experiment. Although enforcing fixation in an online environment is not straightforward, one approach is to use a memory task in which the memoranda are presented so briefly as to preclude the possibility of participants fixating the items. The change detection task, which involves presenting the memoranda for brief periods (~150) and establishing memory capacity (K) rather than memory span (Cowan, 2001) is one such paradigm. Given that the location of the change is unknown at the start of the trial, and that initial eye-movement in displays of multiple, homogenous objects typically has a latency in the range of 200–250 ms (Findlay, 1997), the change detection paradigm offers a reasonable degree of certainty that participants would be unable to make eye-movements to the memory items, even in an online environment. A second experiment therefore examined the HVA for spatial (changes in object location) and visual (changes in object orientation) short-term memory. If the difference between the HVA in the visual and spatial memory tasks is due to differences in oculomotor strategy during the task, preventing eye-movements should reduce or eliminate this difference.

Experiment 2

Methods

Participants

163 participants were recruited through the Dept of Psychology Participant pool and social media, of whom 75 completed the Spatial memory task (10 male, 65 female; median age 20 years) and 88 completed the Orientation memory task (24 males, 63 females, 2 did not state a gender, 1 non-binary; median age 21.01 years). People who took part via the participant pool were awarded pool credit. No compensation was offered to other participants. All participants gave informed consent via an online consent form. The study was approved by Durham University Dept. of Psychology Research Ethics Committee (PSYCH-2021-04-08T13:13:08-dps1ds).

Stimuli and apparatus

Participants completed the experiment on their own personal computer or laptop. Experimental stimuli were generated using PsychoPy3 (Peirce et al., 2019) and data were collected online using Pavlovia. As the size of stimuli varied depending on the specifications of participant's computers and their distance from the screen, dimensions are provided in pixels. The fixation point was as white cross (20 × 20) presented at the centre of the screen. In both tasks the memory array comprised 8 white objects aligned along either the horizontal or vertical midline, such that 4 fell in each hemifield. In the spatial memory task the stimuli were white discs (15 × 15) that appeared 40, 120, 200 and 200 pixels from fixation along the horizontal or vertical meridian, with a random jitter of −30 to +30 pixels applied to the X and Y position. The target was a change in position of one of the objects, which moved its position by 60 pixels in the direction orthogonal to the axis along which the stimuli were presented, such that it crossed the meridian In the orientation memory task the items were 9 × 25 pixel lozenges that appeared 40, 120, 200 and 200 pixels from fixation along the horizontal or vertical meridian. No jitter was applied to these objects. Their orientations were drawn from 8 possible orientations (0, 40°, 80°, 120°, 160°, 200°, 240°, 280° degrees). The target was an orientation change of 80°.

Procedure

The orientation of the memory array was randomized across trials. Trials began with the appearance of a fixation point for 1000 ms. This was replaced by the stimulus array for 150 ms. There was then a 1000 m blank during which the fixation cross was presented. The stimulus array then re-appeared. On 50% of trials one of the objects had changed. In the spatial task, there was a 50% chance of one the objects having. In the Orientation condition, there was a 50% chance of one the objects having moved its orientation by 80°. The change was equally likely to occur at all item positions. The array remained on the screen until the participant made a response by pressing "C" to indicate a change or "N" for no-change. There was 1 block of 32 practice trials and six blocks of 32 experimental trials. Participants were given feedback on their performance during the practice trials but not the experimental trials. Each participant completed 46 change trials and 46 no-change trials on each axis (Figure 3).

Results

Memory capacity was calculated for the horizontal and vertical conditions of the spatial and orientation task using Pashlers' *K* (K_p = Number of Items* (Hit

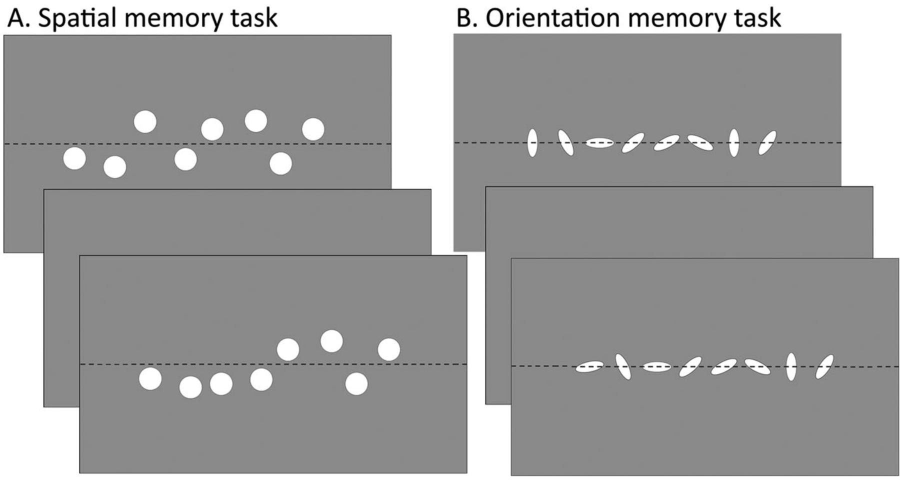

Figure 3. Illustration of the procedure in Experiment 2 in the horizontal condition. The dotted line shows the horizontal meridian and was not visible during the experiment.

Rate – False Alarm Rate) / (1 – False Alarm Rate)). In line with a preregistered analysis plan (OSF Registries | A Horizontal Vertical Anisotropy in Visuospatial Short-Term Memory, Study 1), participants were excluded from the analysis where $K < 1$ for either the horizontal or vertical condition. This resulted in the exclusion of 10 participants from the spatial condition and 41 participants from the orientation condition.

The remaining data were analysed with a 2 (Orientation) × 2 (Task) mixed ANOVA. There were significant main effects of Task ($F_{(1,110)} = 122$, $p < .001$, $\eta^2 p = .53$) and Orientation, ($F_{(1,110)} = 6.2$, $p = .014$, $\eta^2 p = .053$), and a significant Task × Orientation interaction $F_{(1,110)} = 5.05$, $p = .027$, $\eta^2 p = .042$, representing a small effect size. Analysis of simple main effects indicated a significant difference between the horizontal and vertical conditions in the spatial memory task ($M_{hor} = 4.97$, SD = 1.38; $M_{ver} = 4.47$, SD = 1.53; $F = 14.23$, $p = .001$) such that memory spans along the horizontal axis were significantly longer compared to memory spans along the vertical axis. There was no significant difference between the horizontal and vertical conditions in the orientation memory task ($M_{hor} = 2.38$, SD = .87; $M_{ver} = 2.36$, SD = .877; $F = .02$ $p = .88$). Figure 4 illustrates these effects.

Discussion

Experiment 2 explored whether preventing participants from making eye-movements towards the spatial location of targets would elicit a HVA in visual STM. It did not. Similar to Experiment 1, spatial STM capacity was greater for horizontally than vertically aligned stimuli, whereas the axis of presentation made no difference to visual STM capacity. These results are not consistent with the idea that the failure to observe a HVA for visual STM was due to differences in eye-movements.

General discussion

It was hypothesized that visuospatial STM would exhibit a HVA. This prediction was confirmed for spatial STM in both experiments. However, neither experiment found evidence of a HVA in visual STM. The spatial HVA is consistent with the idea that the maintenance of spatial position is mediated by

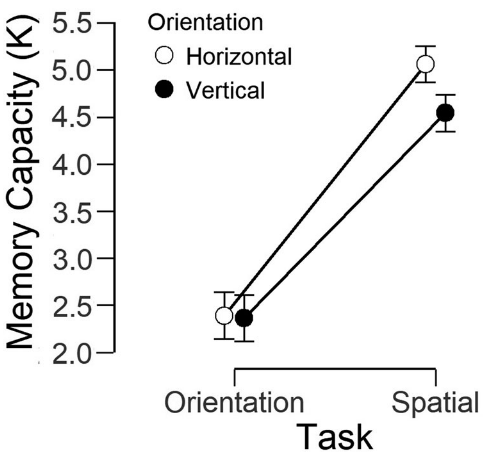

Figure 4. Spatial and visual short-term memory capacity for horizontally and vertically aligned stimuli. Error bars show 95% confidence intervals.

activation in the spatial maps that integrate visual and oculomotor representations into a single, topographic map of space (Bisley & Goldberg, 2010; Ikkai & Curtis, 2011; Zelinsky & Bisley, 2015). The spatial precision of representations in the priority map is likely influenced by the precision with which spatial locations are encoded in the visual and oculomotor system, and it has been shown that spatial coding is less precise along the vertical axis compared to the horizontal axis (Greenwood et al., 2017; Irving & Lillakas, 2019). Given the relative loss of spatial precision for vertical relative to horizontal locations, the observation that spatial spans are reduced along the vertical compared to horizontal axis may be explained in terms of a HVA in the perceptual and oculomotor maps that code spatial position which is inherited by the priority map. This asymmetry results in less precise representation of spatial position along the vertical meridian, and therefore worse memory performance (Lilienthal et al., 2018; Wynn et al., 2019) compared to the horizontal meridian.

In this context the failure to observe a HVA for colour or orientation was surprising, especially given that previous studies have shown that there is a HVA for orientation discrimination (Barbot et al., 2021; Rovamo et al., 1982), and perceptual HVAs can be inherited by VSTM (Montaser-Kouhsari & Carrasco, 2009). It was speculated the null result in Experiment 1 was due to differing eye-movement strategies but Experiment 2 removed the possibility for different overt exploration strategies and still found a null result. It is also possible that the visual STM tasks were too hard, resulting in a floor effect; memory performance was significantly worse and the exclusion rate for poor performance was much higher in the visual STM compared to spatial STM conditions in both experiments.

An alternative interpretation of the HVA in spatial STM and null effect in visual STM is that it reflects a bilateral field advantage. The bilateral field advantage describes an advantage in attention and working memory when stimuli are presented across two hemifields, rather than in a single hemifield (Alvarez et al., 2012; Alvarez & Cavanagh, 2005; Delvenne, 2005; Umemoto et al., 2010) or along the vertical midline (Fendrich et al., 1996), which appears to be specific to spatial, rather than feature representations. This explanation is consistent with Experiment 1, in which the condition in which spatial STM span was higher was also that in which items were distributed equally in the left and right visual fields. Interestingly, it has recently been shown that maintenance of spatial information is more difficult when items move between left and right hemifields than between upper and lower hemifields (Strong & Alvarez, 2020). This "crossover cost" may also have contributed to the significant spatial HVA observed in Experiment 2, in which participants had to detect a target that jumped from one hemifield to another. However, it should be noted that Umemoto et al. (2010) demonstrated a bilateral advantage for orientation using a continuous report task, which is not entirely consistent with the null result for the orientation memory task in Experiment 2.

To summarize, this study provides evidence for a horizontal–vertical anisotropy in spatial STM which persisted when exploratory eye-movements during encoding were prevented. One explanation for this anisotropy is that it reflects poorer spatial coding of locations along the vertical relative to horizontal meridians. An alternative but not necessarily mutually exclusive interpretation is that it reflects a bilateral field advantage for spatial short-term memory. Overall these data are consistent with the view that spatial STM relies on spatial maps that integrate visual and oculomotor signals into a priority map that represents the locations of behaviourally relevant locations.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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