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Holt, JL and Delvenne, JFCM orcid.org/0000-0002-1990-9738 (2015) A bilateral advantage for maintaining objects in visual short term memory. Acta Psychologica, 154. pp. 54-61. ISSN 0001-6918

https://doi.org/10.1016/j.actpsy.2014.11.007

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Volume 154, January 2015, Pages 54-61

A bilateral advantage for maintaining objects in visual short term memory

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Abstract

Research has shown that attentional pre-cues can subsequently influence the transfer of information into visual short term memory (VSTM) (Schmidt, B., Vogel, E., Woodman, G., & Luck, S. (2002). Voluntary and automatic attentional control of visual working memory. Perception & Psychophysics, 64(5), 754-763). However, studies also suggest that those effects are constrained by the hemifield alignment of the pre-cues (Holt, J. L., & Delvenne, J.-F. (2014). A bilateral advantage in controlling access to visual short-term memory. Experimental Psychology, 61(2), 127-133), revealing better recall when distributed across hemifields relative to within a single hemifield (otherwise known as a bilateral field advantage). By manipulating the duration of the retention interval in a colour change detection task (1s, 3s), we investigated whether selective pre-cues can also influence how information is later maintained in VSTM. The results revealed that the pre-cues influenced the maintenance of the colours in VSTM, promoting consistent performance across retention intervals (Experiments 1 & 4). However, those effects were only shown when the pre-cues were directed to stimuli displayed across hemifields relative to stimuli within a single hemifield. Importantly, the results were not replicated when participants were required to memorise colours (Experiment 2) or locations (Experiment 3) in the absence of spatial pre-cues. Those findings strongly suggest that attentional pre-cues have a strong influence on both the transfer of information in VSTM and its subsequent maintenance, allowing bilateral items to better survive decay.

Keywords: visual short-term memory; visual working memory; bilateral field advantage; attention

1.0 Introduction

Visual short term memory (VSTM) allows visual information to be maintained across intervals when no longer in view and thus plays a crucial role in many cognitive tasks. However, the capacity of this store is extremely limited, with most studies revealing that only 3-4 objects can be maintained at any one time (Luck & Vogel, 1997; Vogel, Woodman & Luck, 2001). In order to deal with this limited capacity store, humans must therefore prioritise the relevant information to be processed. The process which selects relevant information in the environment and subsequently maintains the information in memory has been recognised to heavily rely on attention. In fact, attention has even been described as a 'gatekeeper' of VSTM due to its ability to determine which information can enter the store (Awh, Vogel & Oh, 2006).

The role of attentional selective processes on VSTM representations has been extensively studied with the use of the cueing paradigm. For instance, a number of studies have demonstrated that directing attention to the location of one stimulus before encoding, with the use of spatial pre-cues, subsequently improves the chance that the item is transferred into VSTM (Botta, Santangelo, Raffone, Lupiáñez, & Belardinelli, 2010; Griffin & Nobre, 2003; Makovski & Jiang, 2007; Murray, Nobre & Stokes, 2011; Schmidt et al., 2002). Indeed, Murray and colleagues (2011) have recently demonstrated that neural activity associated with preparatory attention at the pre-cueing stage, can predict individual differences in the cue related advantage in VSTM recall. In addition, their findings revealed that the cue related advantage was associated with a specific electrophysiological correlate of VSTM maintenance indicating the number of items within VSTM (otherwise known as contralateral delay activity (CDA), see Vogel & Machizawa, 2004). Research also suggests that directing attention to task relevant stimuli at encoding can subsequently modulate activity in sensory cortices which code those stimuli (for a review see Gazzaley & Nobre, 2012). This top-down modulation has also been shown to directly influence VSTM performance (Rutman, Clapp, Chadwick & Gazzaley, 2009; Zanto, Rubens, Thangavel, & Gazzaley, 2011).

Furthermore, numerous studies have indicated that attentional directing spatial cues are also effective when presented during the maintenance stage of VSTM tasks. Specifically, those studies have shown that directing attention to the location of one previously encoded stimulus using retrocues subsequently enhances the recall of that stimulus (Berryhill, Richmond, Shay & Olson, 2012; Delvenne, Cleeremans, & Laloyaux, 2010; Griffin & Nobre, 2003; Landman, Spekreijse & Lamme, 2003; Lepsien, Griffin, Devlin & Nobre, 2005; Lepsein & Nobre, 2006; Makovski & Jiang, 2007; Makovski, Sussman & Jiang, 2008; Matsukura, Luck & Veraca, 2007; Nobre et al., 2004; Tanoue & Berryhill, 2012; Tanoue, Jones, Peterson & Berryhill, 2013, amongst others). Recent electrophysiological evidence suggests that retro-cues promote the selective access of relevant VSTM representations and bias processing in favour of those representations (Kuo, Stokes & Nobre, 2012). Specifically, Kuo and colleagues (2012) revealed that retro-cues can also modulate the CDA, which in response to retro-cues, reflects the withdrawal of processing resources from irrelevant stimuli and the maintenance of the cued stimuli.

State based models of short-term memory (Cowan, 1995, McElree, 1996; Oberauer, 2002) also propose that attention can play a fundamental role in the short-term retention of information. Specifically, those models reconceptualise the idea of visual short-term memory as active long-term memory, highlighting that attention can influence the representation of items which reside in a common memory store. Indeed, cognitive neuroscience research suggests that memory items inside and outside the focus of attention elicit different neural responses (for a review, see LaRocque, Lewis-Peacock & Postle, 2014).

Recently, we have provided evidence that directing attention simultaneously to the locations of two stimuli, with the use of two separate and non contiguous attentional cues, also improves the chance that those items are transferred into VSTM (Delvenne & Holt, 2012; Holt & Delvenne, 2014). Importantly, the two cues were significantly more effective when they were distributed between the left and right hemifields relative to within the same single hemifield. This supports a number of previous studies that have found that attentional resources are more effectively distributed across hemifields relative to within a single hemifield (Alvarez & Cavanagh, 2005; Awh & Pashler, 2000;

Kraft et al., 2005; Malinowski, Fuchs, & Muller, 2007). Specifically, those studies suggest that the focus of attention can be split to non contiguous locations more easily when the locations are divided across hemifields relative to within a hemifield. The direct implication of this ability to bilaterally split attention is what is known as the bilateral field advantage (BFA), namely an increase of visual processing efficiency when to-be-processed information is divided across the two visual fields relative to when the same information is presented within just one hemifield (e.g. Alvarez & Cavanagh, 2005). This is likely to be an effect of the underlying anatomy of the early visual system which is contralaterally organised (Eviatar & Zaidel, 1994; Gazzaniga, 2000). As the information within each hemifield is initially processed by the contralateral hemisphere, the BFA may be attributed to a processing advantage when stimuli are projected to both cerebral hemispheres rather than one. This advantage in visual processing may be attributed to the interaction of processing resources from each hemisphere (see Banich, 1998) and/or the engagement of independently controlled capacity limited hemispheres (see Alvarez & Cavanagh, 2005) (for a review, see Delvenne, 2012).

Our most recent findings suggest that those hemifield constraints on attentional selection can indeed impact the transfer of information into VSTM (Holt & Delvenne, 2014). By selectively precueing coloured squares in the presence of distracters at encoding, we observed better memory performance when the cued squares were divided across both the left and right hemifields relative to within a single hemifield. Importantly, the BFA was not observed in the absence of those selection requirements, strongly suggesting that the BFA is the result of attentional selection.

Rutman and colleagues (2009) suggest that better VSTM recall in response to pre-cues may be explained by an increase in the fidelity of memory representations due to the early modulation of sensory activity in response to selection. In relation to our previous findings (Holt & Delvenne, 2014), this suggests that bilateral items which are attentionally selected at encoding, may also better survive decay relative to unilateral items. Therefore, the present study investigated whether selective pre-cues can also influence the retention of information in VSTM within and across hemifields. The effect of selective pre-cueing on VSTM maintenance was directly tested by manipulating the retention interval of a memory task (i.e., 1s versus 3s). It was hypothesised that if splitting attention between the left

and right hemifields at the encoding stage provides a benefit on the transfer of the cued items into VSTM but also on their retention, then two bilaterally cued items may better survive decay in memory as compared to two unilaterally cued items.

To preview the results, we found that the BFA was influenced by the duration of the retention interval (Experiment 1 & 4). Interesting the BFA emerged as the retention interval was increased suggesting that bilateral items better survived decay in VSTM. Importantly, this was not shown in the absence of the cues (Experiment 2 & 3), suggesting those effects pertain to the selection of information at the encoding stage. As a result, the findings suggest that selection not only affects the transfer of items into VSTM (Schmidt et al., 2002), but also influences VSTM maintenance. This provides a new understanding of the dynamic relationship between attention and VSTM.

2.0 Experiment 1

2.1 Method

2.1.1 Participants

18 subjects completed the experiment (9 females; mean age = 24.04 years; range= 20-34 years). Participants were neurologically normal with self-reported correct colour vision and normal or corrected-to-normal visual acuity.

2.1.2 Stimuli and procedure

A computer-based change detection task, generated using E-Prime computer software (Psychology Software Tools, Inc., www.pstnet.com) was presented on a 17inch screen of a 3.20GHz PC. Participants were seated at a viewing distance of 60cm and a chin-rest was used to reduce movement. All stimuli were presented on a grey screen background (127 of red, blue and green phosphors) which was divided into 4 invisible quadrants (each subtending 4.8° x 4.8°).

On each trial, participants were presented with a black fixation cross $(.61^{\circ} \times .61^{\circ})$ at the centre of the screen (500ms) followed by the presentation of 12 white placeholders $(.15^{\circ} \times .15^{\circ})$

which were presented at fixed positions across two vertical (unilateral presentation) or two horizontal (bilateral presentation) quadrants indicating the positions of the stimuli to be displayed (500ms). As shown in figure 1, the placeholders within each quadrant were arranged in pairs. The centre-centre distance between each placeholder within a pair was 1.22° . The furthest stimuli from fixation were presented at an eccentricity of 5.76° (centre-centre) and 6.09° to the furthest stimulus edge in the horizontal and vertical directions. The closest stimuli to the vertical and horizontal meridian were presented at a distance of 1.62° centre-centre and 1.29° from each meridian to the nearest stimulus edge.

After 500ms, a placeholder selected at random within each quadrant was enlarged (radius of .34°) cueing the positions of the relevant stimuli to be remembered (50ms). Following a delay of 500ms, 12 coloured squares (.66° x .66°) were presented at the positions of each placeholder (150ms). Repetition of a colour could not occur within one quadrant however repetition across quadrants was possible. The colour of each square was selected from eight possible colours chosen on the basis of discriminability (red, blue, green, yellow, pink, turquoise, orange, and black). Participants were instructed to remember the colours of the two squares that were cued and to ignore the remaining squares. Following the presentation of the memory array, participants were required to maintain the selected information over a retention interval of either 1 second (50% of trials) or 3 seconds. The placeholders remained present throughout the retention interval.

After the retention interval a whole probe test array was presented. In 50% of the trials a cued stimulus changed colour (target change trials) and in the remaining trials a distracter changed colour (distracter change trials). Only one stimulus within one quadrant could change in a given trial. Since participants were required to detect only target changes, distracter change trials were included to discourage the maintenance of distracter stimuli within the memory array and to therefore increase the demands on attentional selection. In 50% of the distracter change trials, the changed distracter was positioned next to a cued stimulus within the same quadrant (near change) at a centre-centre distance of 1.22°. In the remaining trials, the position of the distracter was restricted to the second closest position within the same quadrant from one of the cued stimuli (far change). Therefore, in distracter

change conditions, the distance between the target and the distracter was manipulated within one quadrant of the display. This was manipulated to vary the level of potential distracter interference across trials. The distance of the distracter from the cued stimulus in far change trials was either 2.58°(centre-centre) in the diagonal direction or 3.29° (centre-centre) in horizontal or vertical directions (see figure 2) depending on the position of the cued stimulus. The distance between stimuli across quadrants was always at least 3.24° (centre-centre).

Once the test array was presented, participants were instructed to indicate whether the target colours had changed or stayed the same with a button press (1 = same; 2 = change). They were made aware that in some trials a distracter square could change colour, making it important to precisely select and remember only the target stimuli. Throughout the task, participants were required to rehearse three digits on each block of trials in order to evoke articulatory suppression.

As outlined above, the experiment had a 2(change: distracter, target) x 2(display: bilateral, unilateral) x 2 (retention interval: 1000ms, 3000ms) repeated measures design. Each condition consisted of 32 trials resulting in a total of 256 trials which were randomly distributed in 8 blocks of 32 trials.

Figures 1 & 2

2.1.3 Electrooculography (EOG)

Horizontal eye-movements were recorded using Electrooculography (EOG) with BIOPAC systems. Before the experiment, each participant completed a calibration task to gage the voltage of a 1° horizontal eye-movement. This was then used as a criterion to remove subsequent trials where the eyes moved 1° from fixation in the horizontal or diagonal direction (the closest stimulus from fixation was 1.62° (centre-centre) in the horizontal direction). On each trial, eye-movements were monitored from the onset of the placeholders to the offset of the memory array.

2.2 Results

One participant was removed from the data since mean response accuracy was two standard deviations below the mean response rate (mean= 80.64%, SD= 9.48%, range= 61.27% - 93.90%) Horizontal eye-movements greater than 1° constituted 13.60% of trials which were removed from the data. There was no difference in the number of bilateral versus unilateral trials removed [t(16)= 1.15, p=.27]. In addition, participant trial rejection rates were within two standard deviations from the mean rejection rate (mean = 13.60%, SD= 1.75%, range = 10.54% - 16.79%) and therefore all participants were included in the following analyses.

The analysis was conducted on accuracy and A' from signal detection theory (Aaronson & Watts, 1987; Grier, 1971; Pollack & Norman, 1964). Since both analyses revealed a similar pattern of results the analysis below reports only A'. Performance was analysed in 2 (display: bilateral, unilateral) x 2 (retention interval: 1 s, 3 s) repeated measures ANOVA. The results revealed no effect of retention interval or change however a main effect of display was revealed [F (1, 6) = 7.76, p<.02] which showed a significant BFA with increased accuracy in bilateral relative to unilateral conditions. Importantly, this effect interacted with retention interval [F (1, 16) = 8.38, p < .02]. Paired sample t-tests revealed a significant BFA at three seconds [t(16)= 3.33, p <.005] however no hemifield effects were observed at one second (p=.46). This seems to be accounted for by a tendency towards a decrease in unilateral performance over time [t(16)= 1.92, p=0.07 marginally significant] together with sustained performance across retention intervals in bilateral processing conditions (p= .15) (see figure 3).

With previous research highlighting greater spatial resolution within the lower visual field relative to the upper visual field (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001) and hemispheric asymmetries in visual spatial processing (for a review see Jager & Postma, 2003), visual field asymmetries in performance were also assessed. Although no difference was shown between unilateral performance in the left and right hemifields, paired sample t-tests did reveal better performance in bilateral trials within the lower visual field relative to the upper visual field [t(16)= 3.17, p<.01] which therefore may be accounted for by the demands on spatial precision in the present

task. Hemifield asymmetries were also analysed as a function of retention interval in a series of 2(visual field: upper, lower/ left, right) x 2(retention: 1s, 3s) repeated measures ANOVAs. However no significant interactions were revealed.

Figure 3

2.2.1 Distracter interference

Within the distracter change trials, 50% of distracter changes were positioned near to the target whereas in the remaining trials, distracter changes were positioned far from the target. As a result, it might be expected that near change trials produce a greater level of interference on change detection performance relative to far change trials. In order to investigate whether the BFA was influenced by this factor, accuracy was analysed in a 2(distracter distance: near, far) x 2(display: bilateral, unilateral) x 2(retention: 1s, 3s) repeated measures ANOVA. Although the results revealed a significant effect of display [F(1, 16)= 8.06, p< .02], no effect of distracter distance or interactions were observed. Specifically, the analysis revealed a BFA across all trials despite revealing better performance in far change trials relative to near change trials. Therefore, the results revealed no effect of distracter interference on the BFA.

2.3 Discussion

The findings of Experiment 1 revealed that VSTM for spatially selected colours was better when items were displayed bilaterally relative to unilaterally, replicating our previous findings (Holt & Delvenne, 2014). Importantly however, the BFA was also influenced by the time to maintain those selections in memory. By increasing the retention interval from one to three seconds, we observed that BFA emerged at only the longest retention interval, whereas no hemifield effects were observed at the shortest retention interval. The results also revealed that unilateral performance decreased with time whereas bilateral performance remained consistent. Therefore, the findings support the hypothesis that selection at encoding can also influence the maintenance of information within VSTM. Specifically, as predicted, the results suggest that the engagement of selective attention at VSTM encoding allows bilateral memory representations to better survive decay.

The absence of the BFA at one second was unexpected considering our recent findings of a BFA in a similar selection-based VSTM study with a retention interval of one second (Holt & Delvenne, 2014, Experiment 1). However, on closer inspection, it can be identified that the absence of the BFA may be explained by differences in the task demands across those studies. In the present task, the stimuli were presented in fixed positions with placeholders visible throughout to facilitate the maintenance of spatial selections. On the other hand, our previous study required participants to maintain spatial selections of stimuli that were presented in random positions without placeholders to assist the maintenance of selection. Therefore, the lower demands on unilateral performance may explain the absence of the BFA at the one second retention interval.

As the maintenance of bilateral versus unilateral representations has not been previously addressed over time, it may be questioned whether the maintenance effects observed here can also be shown in the absence of the selection requirements at encoding. For instance, it may be the case that VSTM rehearsal mechanisms which rely on attention (e.g. Awh et al., 1998) always allow bilateral representations to be sustained at longer retention intervals due to an advantage in distributing attentional resources across hemifields (Alvarez & Cavanagh, 2005; Awh & Pashler, 2000; Kraft et al., 2005; Malinowski, Fuchs, & Muller, 2007). Therefore, in order to draw firm conclusions on the role of attentional selection at encoding, VSTM for the stimuli in the present task was assessed in the absence of those selection requirements (Experiment 2 & 3).

In Experiment 1, participants were required to remember both the locations and the colours of the memory stimuli, raising the possibility that the hemifield effects observed may be accounted for by the maintenance of either of those stimulus domains. Therefore, Experiment 2 investigated whether VSTM for colour alone can explain the maintenance effects observed. Although previous studies have failed to reveal a BFA for colour (Delvenne, 2005; Delvenne, Kaddour & Castronovo, 2011; Mance, Becker & Lui; 2012), those studies assessed colour VSTM at retention intervals of only one second,

leaving the possibility of a BFA at longer retention intervals. Therefore, if colour VSTM plays a role in the findings of Experiment 1, we expect the emergence of a BFA when the retention interval is increased to three seconds.

Conversely, previous studies have revealed a BFA in VSTM when participants are required to remember locations (Delvenne, 2005), suggesting the effects shown in Experiment 1 may be accounted for by the requirement to maintain the locations of the memory stimuli. However, as is the case for colour VSTM, the BFA for locations has not been investigated beyond retention intervals of one second. Consequently, Experiment 3 investigated whether VSTM for location alone can produce the hemifield effects observed in Experiment 1. Specifically, if the findings of Experiment 1 can be accounted for by location VSTM then we expected a larger BFA at retention intervals of three seconds relative to one second.

3.0 Experiment 2

3.1 Method

3.1.1 Participants

18 subjects completed the experiment (14 females; mean age = 26 years; range 19-33 years). Participants were neurologically normal with self-reported correct colour vision and normal or corrected-to-normal visual acuity.

3.1.2 Stimuli and procedure

The methodology was the same as Experiment 1 with the exception that the spatial cues and distracter stimuli were not presented (see figure 4). In order to reduce the chance of ceiling effects, colour contrast was added as an additional variable. In 50% of the trials, colours were selected from the 8 high contrast colours presented in Experiment 1. In the remaining trials, low contrast colours were selected from six possible shades of red which were created by manipulating the saturation (S) and luminance (L) values in the following way: (1) L= 100%, S = 100%; (2) L=66%, S=66%; (3) L=33%, S=66%; (4) L=33%, S=100%; (5) L=66%, S=100%; (6) L=100%, S=33%. As only two

colours were presented on each trial, colours were not repeated within the memory array and a new colour was chosen at test in change trials.

Experiment 2 therefore had a 2(colour contrast: high, low) x 2 (display: bilateral, unilateral) x 2 (retention interval: 1, 3) repeated measures design with 32 trials in each condition. Altogether participants completed 256 trials which were randomly blocked into 8 blocks of 32 trials.

Figure 4

3.2 Results

One participant was removed from the data since mean response accuracy was two standard deviations below the mean response rate (mean= 86.70%, SD= 7.4%, range= 61%- 95%). Horizontal eye-movements greater than 1° constituted 13.23% of trials which were subsequently removed from the data. The number of trials removed across each display condition (bilateral, unilateral) [t(16)= -.95, p = .36] and each colour contrast condition (high, low) did not differ [t(16)= .96, p =.35]. In addition, each participant's trial rejection rate was within two standard deviations from the mean rejection rate (mean = 13.23%, SD= 2.91%, range= 8.60% - 18.36%) and therefore all participants were included in the following analyses.

A' was assessed in a 2 (colour contrast: low, high) x 2 (display: bilateral, unilateral) x 2 (retention interval: 1s, 3s) repeated measures design. The results revealed an effect of colour contrast [F(1, 16)=91, p < .001] with greater accuracy in high relative to low contrast conditions, and a main effect of retention interval [F(1, 16)=16.63, p < .002] revealing greater accuracy at one second relative to three seconds. In addition a significant interaction was revealed between colour contrast and retention interval [F(1, 16)=8.11, p < .02]. Paired sample t-test revealed that performance was better at one second relative to three second in both high [t(16)=2.73, p < .02] and low colour contrast condition [t(16)=3.56, p < .005]. However, a larger retention 1s – retention 3s difference score was

revealed in low (4%) relative to high (1.6%) colour contrast conditions [t(16)= -2.29, p <.05]. No other main effects or interactions were shown (see figure 5).

In addition, paired sample t-tests revealed no visual field asymmetries in bilateral (up, down) or unilateral (left, right) displays. Hemifield asymmetries were also analysed as a function of retention interval in a series of 2(visual field: upper, lower/ left, right) x 2(retention: 1s, 3s) repeated measures ANOVAs. However no significant interactions were revealed.

Figure 5

4.0 Experiment 3

4.1 Method

4.1.1 Participants

18 subjects completed the experiment (16 females; mean age = 20.47 years; range= 18-31 years). Participants were neurologically normal with self-reported correct colour vision and normal or corrected-to-normal visual acuity.

4.1.2 Stimuli and procedure

The methodology was the same as Experiment 2, however participants were instructed to remember the locations of the squares presented in the memory array. In order to avoid the rehearsal of colour, the squares remained black throughout the trials. In addition, at test, a single probe was used to discourage participants from memorising the spatial configurations of the memory stimuli. In 50% of the trials, one stimulus moved to a new location which appeared equally within each quadrant, whereas in the remaining trials, the locations of the stimuli did not change. The size of the location change was also manipulated using the same near and far change criteria as in Experiment 1. Therefore, at test, the changed location was either near to (50% of trials) or far from the original location in the memory array.

Consequently, Experiment 3 had a 2 (change: change, no change) x 2 (display: bilateral, unilateral) x 2 (retention interval: 1, 3) repeated measures design with 32 trials in each condition. Altogether, participants completed 256 trials which were randomly distributed into 8 blocks of 32 trials.

4.2 Results

One participant was removed from the data since mean response accuracy was two standard deviations below the mean response rate (mean = 85.48%, SD= 7.81%, range = 68%- 97.3%). Horizontal eye-movements greater than 1° constituted 14.41% of trials and were removed from the data. No difference was shown in the number of bilateral versus unilateral trials removed [t (16) = .55, p = .59] and participant trial rejection rates were within two standard deviations from the mean rejection rate (mean = 14.41%, SD= 2.97%, range = 7.81% - 18.75%)

A' was analysed in 2 (display: bilateral, unilateral) x 2 (retention interval: 1s, 3s) repeated measures ANOVA. The results revealed a main effect of display [F(1, 16)= 14.90, p<.002], highlighting a significant BFA. However, no effect of retention interval and no interaction between retention and display were revealed (see figure 6). Paired sample t-tests also revealed no visual field asymmetries in accuracy across bilateral (up, down) or unilateral (left, right) displays. In addition, hemifield asymmetries were analysed as a function of retention interval in a series of 2 (visual field: upper, lower/ left, right) x 2 (retention: 1s, 3s) repeated measures ANOVAs. However no significant interactions were revealed.

Further analysis investigated whether the size of the location change at test (near, far) influenced the observance of the BFA in a 2 (distance: near, far) x 2 (display: bilateral, unilateral) x 2 (retention: 1s, 3s) repeated measures ANOVA. Although the results revealed an effect of distance [F(1, 16) = 36.93, p<.001] on overall accuracy, with better performance in far change trials relative to near change trials, no interaction with distance was revealed, suggesting that the BFA in the present task cannot be explained by the level of spatial precision required to detect location changes.

Figure 6

4.3 Discussion

The results of Experiments 2 and 3 suggest that the sustained bilateral performance and thus the emergence of the BFA at three seconds shown in Experiment 1 cannot be solely accounted for by the maintenance of colour or locations in VSTM. In Experiment 2, both high and low contrast colours were used in order to avoid possible ceiling effects. However, despite an increase in difficulty with low contrast colours and an overall reduction in accuracy over time, no hemifield effects were observed, supporting previous failures to reveal a BFA for colour VSTM (Delvenne, 2005; Delvenne et al., 2011; Mance et al., 2012).

On the other hand, Experiment 3 revealed that memory for locations produced an overall BFA, supporting previous demonstrations of a BFA in location VSTM (Delvenne, 2005). Therefore, the requirement to remember the target locations in Experiment 1 may have also contributed to the BFA observed. However, the overall effect of retention interval shown in Experiment 3 suggests that both unilateral and bilateral representations decayed the same amount with time, indicating that the maintenance effects in Experiment 1 cannot be simply explained by the maintenance of locations in VSTM.

Therefore, the results suggest that the findings of Experiment 1 are likely to be attributed to the encoding requirements of the task. As well as the presence of pre-cues at encoding, it can also be recognised that participants were required to ignore distracter stimuli in the array. Consequently, it is likely that the distracters placed a greater demand on the ability to precisely select items at the encoding stage. Therefore, Experiment 4 addressed whether the results of Experiment 1 can also be replicated when the distracters are removed from the array and thus the memory items are solely precued at the encoding stage. If the effects of Experiment 1 are replicated, then the findings strongly suggest a role of the attentional pre-cues in the maintenance of items within VSTM.

5.0 Experiment 4

5.1 Method

5.1.1 Participants

18 subjects completed the experiment (13 females; mean age = 22.74 years; range = 19-35 years). Participants were neurologically normal with self-reported correct colour vision and normal or corrected-to-normal visual acuity.

5.1.2 Stimuli and procedure

The trial procedure was the same as Experiment 2, however the memory array was preceded by the presentation of two spatial pre-cues (50ms) with a cue-to-target delay of 500ms in which the placeholders were presented alone. To avoid possible ceiling effects, only low contrast colours were used in the memory array. Therefore, the experiment had a 2 (display: bilateral, unilateral) x 2 (retention: 1s, 3s) repeated measures design with 32 trials in each condition. In total, participants completed 128 trials which were randomly distributed into 4 blocks.

5.2 Results

Mean response accuracy for all subjects was within two standard deviations below the mean and so all subjects were included in the following analysis (mean= 81.74%, SD= 4.9%, range= 73.9%- 89.3%). Horizontal eye-movements greater than 1° constituted 13.85% of trials and were removed from the data. No difference was shown in the number of bilateral versus unilateral trials removed [t (17) = .26, p = .80] and participant trial rejection rates were within two standard deviations from the mean rejection rate (mean= 13.85%, SD= 2.93%, range= 8.59% - 17.97%).

A' was analysed in a 2 (display: bilateral, unilateral) x 2 (retention interval: 1s, 3s) repeated measures ANOVA. The results revealed an effect of retention interval [F(1, 17)=18.82, p<.001] showing greater accuracy at one second relative to three seconds and a main effect of display was shown [F(1, 17)=5.60, p<.05] highlighting a significant BFA. Importantly, a significant interaction

between retention and display [F(1, 17)= 4.84, p<.05] was revealed. Paired sample t-tests showed a significant BFA at three seconds only [t (17) = 2.92, p<.02], however no hemifield effects were shown at one second (p=.70). In addition, paired sample t-tests showed that unilateral performance declined as the retention interval increased [t (17) = 4.04, p<.001], where as the difference in performance across retention intervals was marginally significant for bilateral performance [t (17) = 1.88, p = .08] (see figure 7).

Further analysis revealed no visual field asymmetries in accuracy across bilateral (up, down) or unilateral (left, right) displays. In addition, hemifield asymmetries were analysed as a function of retention interval in a series of 2(visual field: upper, lower/ left, right) x 2(retention: 1s, 3s) repeated measures ANOVAs. However no significant interactions were revealed.

Figure 7

5.3 Discussion

The results of Experiment 4 replicated the findings of Experiment 1, revealing a BFA that was influenced by the duration of the retention interval. Again, the pattern of performance revealed that the BFA emerged at the longest retention interval only indicating that bilateral accuracy was consistent whereas unilateral accuracy reduced over time. In contrast to Experiment 1, an effect of retention interval was shown overall. This may be due to the fact that only low contrast colours were presented in Experiment 4, which as the results of Experiment 2 indicate, decay to a greater extent relative to high contrast colours across the retention interval.

Due to the absence of hemifield effects for colour VSTM without spatial pre-cues (Experiment 2), the results strongly suggest the way an item is encoded can affect how it is maintained. Specifically, the results suggest that the attentional directing pre-cues at encoding allow bilateral items to better survive decay.

6.0 General discussion

Recent research has shown that the requirement to attentionally select items during both the encoding (e.g. Schmidt et al., 2002) and maintenance (e.g. Griffin & Nobre, 2003) stage of VSTM tasks can subsequently improve the ability to recall those items at test. However, our findings suggest that when two cues are used, their effects are constrained by the hemifield alignment of the selected items (Delvenne & Holt, 2012; Holt & Delvenne, 2014). Specifically, our findings suggest that two cues are more effective when they are divided between hemifields relative to when both cues are displayed within a single hemifield (otherwise known as a Bilateral Field Advantage (BFA), see Alvarez & Cavanagh, 2005). Our most recent findings (Holt & Delvenne, 2014) suggest that those constraints influence the transfer of information into VSTM, revealing a BFA in recall for items that are selectively pre-cued at encoding. Given that selection may also influence the maintenance of information in VSTM (Gazzaley & Nobre, 2012; Rutman et al., 2009; Zanto et al., 2011), the present study investigated whether bilateral items can better survive decay in VSTM relative to unilateral items when attentionally selected at encoding.

Supporting our previous findings (Delvenne & Holt, 2012; Holt & Delvenne, 2014), the present study revealed that selecting targets from distracters promoted a BFA, with better recall in bilateral relative to unilateral conditions. Importantly however, the findings indicated that the magnitude of the BFA also increased with longer retention intervals (Experiments 1 & 4), strongly suggesting that selection at encoding can influence the maintenance of items in VSTM. Specifically, whereas unilateral performance decreased with time, we observed no decrease in bilateral performance, indicating that selection allowed bilateral representations to better survive decay. Further experiments revealed this could not be accounted for by an effect of VSTM maintenance in the absence of the selection requirements (Experiment 2 & 3). Instead, the findings suggest that those effects emerge when stimuli are simply pre-cued at encoding (Experiment 4).

Observing a cue-related advantage in VSTM recall, Rutman and colleagues (2009) suggest that the early modulation of activity in response to selective attention may increase the fidelity of the representations which thus translates to better maintenance across the retention interval. Our findings provide a clearer understanding of this contention, revealing specifically that cued items can better survive decay. An investigation at the neural level is required to provide a further understanding of those effects. However, since the maintenance of items within VSTM also relies on sustained activity in sensory areas that code the stimuli (Harrison & Tong, 2009; Serences, Ester, Vogel and Awh, 2009; Xing, Ledgeway, McGraw & Schluppeck, 2013), one possibility may be that early modulations in visual sensory areas in response to the pre-cues (e.g. Gazzeley & Nobre, 2012; Rutman et al., 2009; Zanto et al., 2011) influence the persistence of maintenance activity during the retention interval.

Previous research suggests that the number of items maintained in VSTM can be measured online by recording contralateral delay activity (see Vogel & Machizawa, 2004) during the retention interval. The CDA reflects the number of items maintained from the contralateral hemifield with respect to the hemisphere recorded, and therefore heavily relies on the existence of lateralised visual memory processing as previously proposed (e.g. Eimer & Kiss, 2010; Gratton, Corballis, & Jain, 1997; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicœur, 2012). Supporting this account, Arend and Zimmer (2011) recently provided evidence against the contention that the CDA may reflect items displayed in both the left and right hemifields, highlighting that the lateralisation of visual memory is maintained even at the end of the retention interval. Revealing a larger BFA as the retention interval increased, the present findings support Arend & Zimmer (2011), suggesting that hemifield representations can be maintained in VSTM for up to three seconds. As a result, the findings suggest that neuronal investigations of bilateral VSTM representations may benefit from assessing each hemisphere separately (for a demonstration, see Delvenne et al., 2011).

It is evident that previous research has raised a number of questions concerning the nature of the BFA in VSTM, with studies exploring the influence of stimulus domain (Delvenne, 2005; Delvenne et al., 2011; Holt & Delvenne, 2014) and the stage of VSTM processing (Holt & Delvenne, 2014; Kraft, 2013; Umemoto et al., 2010) which influence the emergence of the BFA. In observing a BFA in colour VSTM when selective processes were engaged (Experiment 1 & 4), the present study provides confirmatory evidence that the BFA is not only constrained by the stimulus domain, but is a signature of attentional selection (Holt & Delvenne, 2014). As previously discussed, the BFA may be explained by the increased ability to distribute attention across hemifields relative to within (Alvarez & Cavanagh, 2005; Awh & Pashler, 2000; Kraft et al., 2005; Malinowski et al., 2007)

Furthermore, in demonstrating a BFA during the maintenance stage, the present findings support the notion that the BFA is a feature of mnemonic processing (Kraft, 2013) and can specifically arise within VSTM storage (Umemoto et al., 2010). As suggested by Umemoto and colleagues (2010), the emergence of the BFA within VSTM storage may also be attributed to engagement of spatial selection in VSTM rehearsal (e.g. Awh, Jonides & Reuter-Lorenz, 1998; Williams, Pouget, Boucher, & Woodman, 2013). However, since the present findings identified that the BFA in maintenance was contingent on the presence of pre-cues at encoding (Experiment, 4), the findings suggest that the BFA within maintenance may also be influenced by the engagement of selection mechanisms during perception.

Indeed, Corbetta, Kincade and Shulman (2002) revealed that selective attention in perception and working memory maintenance recruit a similar neural circuitry, supporting the deployment of a common attentional mechanism at both stages (Awh, Anllo-Vento, & Hillyard 2000; Awh et al 1999; Jha, 2002; Postle, Awh, Jonides, Smith, & D'Esposito, 2004). Therefore, it is plausible that the nature of selection during encoding, specifically a divided attentional distribution to non contiguous locations, was maintained during VSTM maintenance and thus allowed bilateral representations to survive decay. However at present, a direct assessment of attentional processes during maintenance (e.g. Fougnie & Marois, 2009) is required to confirm this hypothesis.

Future research may also address the extent of VSTM decay as a function of hemifield alignment across variable retention intervals and stimulus domains. It is evident that the present findings are limited to the rehearsal of colour and confined to retention intervals of three seconds. Indeed, the marginally significant effect of decay in the unilateral conditions of Experiment 1 may be reflective of the relatively short retention intervals employed, and as highlighted in Experiment 2, may be influenced by factors such as stimulus contrast. Nevertheless, for the first time, the present findings indicate that bilateral memory representations can be less susceptible to decay relative to unilateral representations, providing a further step to understanding the limits and neuronal architecture of the VSTM store.

6.1. Conclusion

In sum, the present study provides a new understanding of the relationship between attention and memory, suggesting that selective attention at VSTM encoding improves both the transfer of information into the VSTM store (Schmidt et al., 2002) and the subsequent maintenance of the information within VSTM. Importantly, with hemifield constraints in the deployment of spatial attention, those effects are limited by hemifield alignment, highlighting the importance of considering the spatial distribution of information when investigating the relationship between spatial attention and VSTM processing (Delvenne & Holt, 2012; Holt & Delvenne, 2014).

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Fig.1. An illustration of the fixed positions in the bilateral and unilateral displays of Experiment 1.
For clarity, the illustration is not drawn to scale.



Fig. 2. The trial procedure of Experiment 1. The arrows in the test array indicate distracters which are located in far and near positions relative to the cued targets within each quadrant. For clarity, the illustration is not drawn to scale.



Fig. 3. Results of Experiment 1. A' as a function of retention interval (1000ms, 3000ms) and display (bilateral, unilateral). Error bars represent the standard error of the mean values.



Fig. 4. The trial procedure of Experiment 2. For clarity, the illustration is not drawn to scale.



Fig. 5. Results of Experiment 2. A' as a function of colour contrast (high, low), retention (1000ms, 3000ms) and display (bilateral, unilateral). Error bars represent the standard error of the mean values.



Fig. 6. Results of Experiment 3. A' as a function of retention interval (1000ms, 3000ms) and display (bilateral, unilateral). Error bars represent the standard error of the mean values.



Fig. 7. Results of Experiment 4. Percentage of correct responses and A' as a function of retention interval (1s, 3s) and display (bilateral, unilateral). Error bars represent the standard error of the mean values.