This is a repository copy of *Visual short-term memory and the bilateral field advantage*.

Book Section:

Visual short-term memory and the bilateral field advantage

Jean-Francois Delvenne

Institute of Psychological Sciences, University of Leeds, U.K.

Abstract

Past research has demonstrated superior visual processing when the information is distributed across the left and right visual fields rather than within the same single hemifield. This effect is known as the *bilateral field advantage* (BFA). Recent studies have recently begun to investigate whether a BFA also arises in visual short-term memory (VSTM), with a direct effect on its storage capacity. In other words, the question is whether it is possible to remember more visual objects when they are distributed between the two hemifields than when they are all located within a single one. The goal of this chapter is to provide a synthesis of the current data regarding the possible existence of a BFA in VSTM. Those data reveal that a BFA can be found in spatial short-term memory, namely when the task requires holding spatial information. However, no BFA has been found in object short-term memory (i.e., when the task is to hold detailed visual properties of the objects), unless attentional selective processes are dominantly engaged in the task, suggesting that the BFA is a general feature of selective attention.

1. Introduction

In everyday life, the transfer of sensory input to the visual system is often interrupted by events such as eye blinks and saccades, or by full or partial occlusions from irrelevant information. To maintain and integrate relevant visual information across those interruptions, and to draw on this information to guide behaviours, we need a temporary buffer known as *visual short-term memory* (VSTM) (Philips, 1974), or *visual working memory* (Baddeley & Hitch, 1974). VSTM is vital for nearly all cognitive activities. For example, when driving a car, we must incessantly look at our surroundings and remember relevant information, such as the location of the other vehicles on the road to avoid collisions, or the traffic signs to guide driving behaviours. When reading comic strips, we must look at and remember one drawing at a time while we read the short text that relates to it. In any social contacts, such as team sports, conversations, or simply walking in town with our mates for instance, we must encode and remember the identities and the whereabouts of the people around us to properly interact.

Intuitively, we may assume that we can encode and remember a large proportion of information that is presented in our visual field. However, the last decades of research have shown that only a small amount of information can actually reach visual awareness and be stored in VSTM at any one time. Probably the first compelling demonstration of this limitation was provided by Luck and Vogel (1997). In their seminal study, Luck and Vogel used the change detection paradigm (Philips, 1974) in which participants were required to detect a change between two successive visual displays. More specifically, participants were first briefly presented with a memory array containing a number of "objects" (i.e., simple coloured squares or oriented bars). The memory array was then followed by a brief blank screen and finally by the test array. In half of the trials, the objects in the test array were similar as the ones in the memory array, whereas in the other half of the trials, one object was different. Luck and Vogel observed that in average change detection performance was near perfect on array sizes containing up to four objects but dropped dramatically and systematically with larger set sizes. For the last 15 years, those findings have been repeatedly replicated and it is now fairly established that the capacity of VSTM is around 3-4 objects (e.g., Cowan, 2001; Sperling, 1960, Pashler, 1990; Vogel, Woodman, & Luck, 2001; see also the review by Brady, Konkle, and Alvarez, 2011).

The discovery of this capacity limit is not only a laboratory curio. The severe limitation of our VSTM capacity can also be observed in, and has an impact on, our everyday life. For instance, research has shown that gross changes between two seemingly similar visual scenes can often be undetected, a phenomenon known as "change blindness" (e.g., Rensink, O'Regan, & Clark, 1997; Simons & Levin, 1997, 1998). Because the detection of a change requires a comparison of the visual input to a previous representation of the information held in memory, the limitation of VSTM capacity is thought to be at least to a certain extent accountable for this phenomenon. Furthermore, the failure to store in memory more than just a few objects at one time may also explain many human errors that occur in a variety of situations where a large amount of visual information needs to be processed simultaneously. For instance, the capacity limit has been suggested to be linked with road crash risk (e.g., Langham, Hole, Edwards, & O'Neill, 2002).

Since the publication of Luck and Vogel (1997)'s paper, the majority of the research on VSTM has tried to identify the factors that may influence its capacity. Indeed, determining the factors that may improve our processing capacities, such as our mnemonic capacities, has become crucial if one wish to cope effectively with the information-rich environment in which we all live nowadays. Among those factors, there is object complexity (i.e., VSTM capacity decreases as function of object complexity - Alvarez & Cavanagh, 2004), the nature of the features (i.e., VSTM capacity increases

when the to-be-remembered features belong to distinct dimensions, such as colour, shape, orientation, texture, etc., as compared to when they belong to the same dimension – Wheeler & Treisman, 2002; Xu, 2002a, Delvenne & Bruyer, 2004), the perceptual integration (i.e., VSTM capacity increases when the to-be-remembered features are bound into a smaller number of objects as compared to when the features are all separated– Delvenne & Bruyer, 2004; Luck & Vogel, 1997, Olson & Jiang, 2002; Vogel, Woodman, & Luck, 2001; Wheeler & Treisman, 2002), the spatial arrangement of object parts (i.e., VSTM capacity increases when the features belong to the same object parts as compared to different parts - Delvenne & Bruyer, 2004; Xu, 2002b), the configural organisation of the objects within the display (i.e., the encoding of the spatial relationships between the objects benefits VSTM capacity – Delvenne, Braithwaite, Riddoch & Humphreys, 2002; Delvenne & Bruyer, 2006, Jiang, Olson, & Chun, 2000), the third dimension (i.e., VSTM capacity increases when objects are placed in a 3-D space as compared to a 2D space– Xu & Nakayama, 2007), and perceptual expertise (i.e., VSTM capacity increases as function of visual expertise – Curby, Glazek, & Gauthier, 2009; Jackson & Raymond, 2008).

In our visual world, objects can be located at the centre of our visual field, namely within the small region of space that we fix at a particular moment. However, in most cases other objects will also be presented elsewhere within our visual field, specifically to the left or right sides of fixation. Because of the crossing of the neural projections from the retina to the striate cortex, visual information that occurs in one half of the visual field is predominantly processed and represented in the contralateral cerebral hemisphere (see Bullier, 2004; Eviatar & Zaidel, 1994; Manson & Kandel, 1991). Only visual stimuli along the vertical meridian are projected to both hemispheres (Chiang, Walsh, & Lavidor, 2004; Lavidor & Walsh, 2004). As we will see in Section 2, one major effect of this contralateral organization of the visual system is that it allows us to process more effectively the visual inputs when the information is distributed across the left and right hemifields, thus projected to two hemispheres, as compared to when the same information is presented within one hemifield only, therefore projected to a single hemisphere. This phenomenon is known as the *Bilateral Field Advantage* (BFA).

In the VSTM domain, very little is known about how the contralateral organisation of the visual system may influence its storage capacity. In particular, it is not clear whether VSTM capacity is fixed regardless of whether the to-be-remembered objects share the same or different hemifields or whether VSTM capacity may be modulated by the spatial distribution of the objects across the two half visual fields. If the latter were true, it would grant us with a better appreciation of what determines VSTM capacity. It may also help us find ways to improve VSTM capacity, and thus behavioural performance that relies on it in real environments. The goal of this chapter is to provide a synthesis of the current data regarding the possible existence of a BFA in VSTM. I will first review the evidence showing the BFA in visual information processing (section 2). Then, I will review the recent studies that have directly investigated the possible existence of a BFA in VSTM (section 3).

2. Bilateral Field Advantage in visual information processing

The bilateral field advantage (BFA) in visual information processing refers to the fact that visual tasks are processed more quickly and/or more accurately when the visual inputs are distributed across the vertical meridian than when they are all presented within the same single hemifield[1]. Because of the

---

[1] In some studies, the term *bilateral field advantage* has also been used to refer to a distinct phenomenon whereby presenting similar stimuli to both visual fields produces better performance than presenting a single stimulus to either hemifield alone (Baird & Burton, 2008; Miniussi, Girelli, & Marzi, 1998). A phenomenon also called *bilateral redundancy gain*.

contralateral organisation of the visual system, the general interpretation of this phenomenon is that the two cerebral hemispheres possess some degree of processing resources independence. Probably one of the first demonstrations of a BFA was provided 40 years ago by Dimond and Beaumont (1971). The authors used the divided visual field technique in which participants had to report pairs of digits that were briefly presented for 250ms either within the same hemifield or across the two hemifields. The authors observed that a significant higher number of pairs of digits were correctly reported when the stimuli were displayed to both hemifields as compared to only one hemifield. Dimond and Beaumont later confirmed the performance improvement in visual processing capacity for bilateral presentations in a task that employed non-verbal information (Dimond and Beaumont, 1972). In this study, the authors found faster reaction times when participants had to match two complex visuo-spatial figures that occurred in separate hemifields as compared to within the same single hemifield. The two studies of Dimond and Beaumont mentioned here constitute a good illustration of the two main categories of visual tasks that have been used over the years to demonstrate the BFA. Specifically, some tasks have been designed to investigate whether independent processing capacities exist in the left and right hemispheres (section 2.1.). Other tasks have been used to investigate the efficiency of inter-hemispheric interaction (2.2.).

2.1. Bilateral Field Advantage as an index of hemispheric independence

In some studies, the BFA suggests the existence of some degree of independence in visual processing capacity in the left and right hemispheres. Those studies use visual tasks that simply require processing each stimulus independently, in parallel, without the need of processing the information about their relationship to one another. For example, they may be designed to investigate whether a larger number of stimuli can be processed in bilateral arrays as compared to unilateral arrays. The digits report task used by Dimond and Beaumont (1971), in which two stimuli are briefly presented to a single hemifield or one each to a different hemifield, falls into that category. Typically, results reveal the best performance when each stimulus is presented to a different hemifield (i.e., the BFA). The effect has been observed in several studies and holds true whether the task involves identifying digits or letters (Awh & Pashler, 2000; Chakravarthi & Cavanagh, 2006; Scalf, Banich, Kramer, Narechania, & Simon, 2007), detecting simple targets (Castiello & Umilta, 1992; Reardon, Kelly, & Matthews, 2009), searching for a target amongst distracters (Alvarez & Cavanagh, 2006), detecting and discriminating orientations (Chakravarthi & Cavanagh, 2006; Reardon et al., 2009), or even encoding and remembering spatial information (Delvenne, 2005; Umemoto, Drew, Ester, & Awh, 2010 – see section 3).
Probably the most compelling demonstration of a BFA in this category of visual tasks was provided by Alvarez and Cavanagh (2005). Alvarez and Cavanagh used a Multiple Object Tracking task (Pylyshyn & Storm, 1988), in which participants were required to attentionally track a number of moving targets presented amongst moving distracters. When all the targets were presented within the same hemifield, participants could accurately track two targets, but performance dramatically decreased when four targets had to be tracked. By contrast, participants could track four targets as well as two targets if they were distributed in separate hemifields. This shows that in some tasks it is even possible to process twice more objects when they are split between the two half fields, a result rendering possible only if one assume some kinds of hemispheric independence in visual processing.

This notion of hemispheric independence is strengthen by studies of split-brain patients (Gazzaniga & Young, 1967; Holtzman & Gazzaniga, 1985; Luck, Hillyard, Mangun, & Gazzaniga, 1989, 1994). Split-brain patients have their corpus callosum seriously damaged or sectioned after a surgical operation usually undertaken at the last resort for the control of intractable epilepsy. As a result, the two cerebral hemispheres in those patients are unable to exchange visual information and the stimuli presented in one visual field are exclusively processed by the contralateral hemisphere (see Eviatar & Zaidel, 1994). Studies have shown that split-brain patients can either perform better than normal healthy subjects if the visual inputs are distributed between the left and right visual fields (Luck et al., 1989), or exhibit a BFA in their performance while control subjects do not (Luck et al., 1994). For example, using a visual search task, Luck and colleagues (1994) discovered that split-brain patients can scan bilateral stimulus arrays at a much faster rate (twice as fast in some cases) than unilateral arrays. This BFA observed with split-brain patients, however, was not found in normal control subjects, suggesting that the hemispheric independence in processing capacities can sometimes be erased when the two hemispheres are able to exchange information via the corpus callosum. However, as we will see in section 2.2., the unavoidable cost in inter-hemispheric interaction is often too small to erase entirely the benefit of parallel processing by the two hemispheres.

2.2. Bilateral Field Advantage as an index of inter-hemispheric interaction

In everyday life, most visual tasks entail the information from one hemifield to be integrated or compared with the information from the other hemifield. For example, when we enumerate a set of objects placed in our visual field, objects from our left and right hemifields need to be combined in order to obtain a single quantity. This means that at higher levels, the two hemispheres need to exchange information via the corpus callosum (see Bullier, 2004), and this is inevitably accompanied with some costs in processing times or efficiency. In some studies, the BFA particularly refers to the fact that the initial benefits of parallel processing by the two hemispheres outweigh the cost of inter-hemispheric interaction. Those studies use visual tasks that not only involve processing each stimulus individually, but require also the integration or comparison of information presented within or across hemifields. The complex figures matching task used by Dimond and Beaumont (1972), for example, in which two stimuli presented either unilaterally or bilaterally had to be compared, falls into this category. The matching task, as a way to reveal a BFA, has been extensively used in the literature (Banich & Belger, 1990; Belger & Banich, 1992, 1998; Berger, 1988; Brown, Jeeves, Dietrich, & Burnison, 1999; Collin, McMullen, & Seguin, 2009; Compton, 2002; Davis & Schmit, 1971; Koivisto, 2000; Kraft, Muller, Hagendorf, Schira, Dick, Fendrich, & Brandt, 2005; Kraft, Pape, Hagendorf, Schmidt, Naito, & Brandt, 2007; Liederman, Merola, & Martinez, 1985; Ludwig, Jeeves, Norman, & DeWitt, 1993; Muller, Malinowski, Gruber, & Hillyard, 2003; Norman, Jeeves, Milne, & Ludwig, 1992; Reuter-Lorenz, Stanczak, & Miller, 1999; Sereno & Kosslyn, 1991; Weissman & Banich, 2000; Weissman, Banich, & Puente, 2000; Zhang & Feng, 1999). Other studies have also observed the same phenomenon using different types of tasks that also require integration of information presented at different locations within the visual field, therefore involving, in the case of bilateral presentations, inter-hemispheric interaction. For example, Hatta and Tuji (1993) used a task in which participants were required to add numbers. In the same vein, with my colleagues (Delvenne, Castronovo, Demeyere, and Humphreys, 2011a), we have recently found a BFA in a visual enumeration task in which participants were required to enumerate simple dots that appeared briefly on the computer screen.

The BFA appears to be contingent on the complexity or difficulty of the task. Many studies have revealed that the BFA increases, or simply becomes apparent, as the difficulty of the task increases (Banich & Belger, 1990; Belger & Banich, 1992, 1998; Delvenne et al., 2011a; Merola & Liederman, 1990; Norman et al., 1992; Reuter-Lorenz et al., 1999; Weissman & Banich, 2000; Weisman et al., 2000; Zhang & Feng, 1999). For example, in our visual enumeration task, the BFA was only observed when more than four dots had to be enumerated (Delvenne et al., 2011a). Moreover, when the task is relatively simple and does not require many processing resources, a *unilateral field advantage* can sometimes occur (Banich & Belger, 1990; Butcher & Cavanagh, 2008; Hayes, Swallow, & Jiang, 2010; Weisman et al., 2000). For instance, using a letter-matching task, Banich and Belger (1990) observed that when the two letters to be-matched were perceptually identical (e.g., A & A), performance was better for unilateral than bilateral arrays. By contrast, when the letters were perceptually dissimilar (A & a), or when the number of letters displayed on the screen is increased to five (Belger & Banich, 1992), the task difficulty increased and performance was better for bilateral than unilateral arrays. Consistent with these findings, neuroimaging studies have demonstrated that computationally complex tasks often produce more bilateral activities than do simpler tasks (e.g., Awh, Smith, & Jonides, 1995; Klingberg, O'Sullivan, & Roland, 1997; Pollman, Zaidel, & von Cramon, 2003).

In sum, a large body of research, especially over the last two decades, has shown that (1) the two cerebral hemispheres have, at least to some extent, their own independent resources for processing visual information; (2) the independent, parallel processing provides a gain in efficiency if the task is sufficiently demanding and if it recruits both cerebral hemispheres; (3) in most visual tasks, the benefits of this initial hemispheric independence outweigh the cost of exchanging and integrating information between the hemispheres.

3. Bilateral Field Advantage in Visual Short-Term memory

The capacity of VSTM typically refers to the maximum number of items that can be encoded and held in memory simultaneously. However, research suggests that the capacity may not be only defined by the number of memory representations, but also by their precision or resolution. (Alvarez & Cavanagh, 2004; Xu & Chun, 2006; Zhang & Luck, 2008). The number and resolution of memory representations may even represent distinct and independent aspect of VSTM. For example, Xu and Chun (2006) found that the neural regions that are sensitive to the number of memory items (i.e., inferior intraparietal sulcus) are distinct from those that are sensitive to the complexity of the stored items (i.e., superior parietal and lateral occipital cortex). Therefore, a BFA in VSTM implies that the distribution of visual information across both hemifields increases the maximum number of items that can be encoded and held in memory simultaneously, and/or improves the resolution of their representations compared to when the items occupied the same single hemifield.

While the existence of a BFA in visual processing is pretty much well established nowadays (see section 2), the question of whether the BFA extends to memory only started to be directly addressed a couple of years ago and, as we will see, reveals conflicting findings. Yet, reasons as to why a BFA can be expected in VSTM are to be found in the close relationship between VSTM (the 'off-line' processing) and perception (the 'online' processing). A growing body of neuroimaging (Awh & Jonides, 2001; Harrison & Tong, 2009; Postle, 2006; Serences, Ester, Vogel & Awh, 2009) and single-unit studies (Miller, Erickson, & Desimone, 1996; Supèr, Spekreijse, & Lamme, 2001) suggests that the early cortical regions recruited to encode sensory information are also sustainably activated during VSTM storage. Thus, visual objects are represented in brain areas where object processing occurs. In the same vein, it has been proposed that the contralateral organization of the visual system extends in VSTM, where information presented in one hemifield is maintained by sustained activity in the contralateral visual cortex (see Gratton, 1998; Gratton, Corballis, & Jain, 1997). Much

evidence comes from recent event-related potentials studies that have identified a specific contralateral electrophysiological correlate of the contents of VSTM (Delvenne, Kaddour, & Castronovo, 2011b; Eimer & Kiss, 2009; Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006a, 2006b; Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; McCollough, Machizawa & Vogel, 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). In those studies, participants are presented with a number of visual items to both sides of fixation and are required to memorize the items of either the left or right side. A sustained posterior negative wave is observed throughout the memory retention period, which is larger over the contralateral side of the brain (with respect to the position of the memory items in the visual field) relative to the ipsilateral side. Importantly, the amplitude of this contralateral delay activity (CDA – also called SPCN, for sustained posterior contralateral negativity) increases progressively with the number of items to be remembered, reaching an asymptotic limit at around three-four items. The contralateral organization of visual memories raises logically the possibility that each hemisphere has its own capacity of storage.

In addition, as mentioned in section 2.1., the clearest demonstration of a BFA in visual processing was provided in an attentional tracking task (Alvarez & Cavanagh, 2005), where the overall tracking capacity (i.e., around 4 objects) was equal to the sum of two independent tracking capacities, one in each hemisphere (i.e., around 2 objects). For the last ten years, numerous behavioural and neuroimaging studies have found a functional overlap between attentional tracking and VSTM. Not only do they share the same overall capacity limit of approximately 3-4 objects (Alvarez & Cavanagh, 2005; Luck & Vogel, 1997; Oksama & Hyönä, 2004; Pashler, 1988; Pylyshyn & Storm, 1988), but they also correlate in an individual's performance (Oksama & Hyönä, 2004) and interfere each other when participants have to simultaneously attentionally track and remember objects in VSTM (Fougnie & Marois, 2006). Functional MRI studies have also identified similar brain regions (i.e., intraparietal sulcus and frontal eye fields) activated during both tracking and VSTM tasks (Culham, Cavanagh, & Kanwisher, 2001; Todd & Marois, 2004; 2005; Xu & Chun, 2006) and event-related potentials studies have found similar waveforms (i.e., the CDA) (Drew & Vogel, 2008; Vogel & Machizawa, 2004).

3.1. Empirical evidence

3.1.1. Evidence supporting the Bilateral Field Advantage in Visual Short-Term memory

In 2001, Gratton and colleagues (Gratton, Fabiani, & Corballis, 2001) briefly reported unpublished data in which they found a BFA in a VSTM task. Specifically, the authors used a recognition task where a number of patterns of randomly oriented lines were sequentially presented on a computer screen for 200 ms each and separated by an 800 ms interval. Following the memory set (that consisted of 5 stimuli), a test stimulus was presented at the centre of the screen and the task was to decide whether the stimulus belonged to the memory set. The results showed that the participants were faster at recognizing the test stimulus as being part of the memory set when the memory set stimuli were distributed across the left and right hemifields as when they were presented unilaterally.

However, to the best of my knowledge, there are currently only two published studies in humans that have provided a clear demonstration of a BFA in VSTM. The first study that directly investigated this question was the one I conducted a couple of years ago (Delvenne, 2005). I used a standard change detection task in which a number of squares were simultaneously and briefly presented for 200 ms either within the same hemifield (*unilateral condition*) or across both hemifields (*bilateral*

condition). Following a short retention interval of 1000 ms, the stimuli reappeared and the participants had to detect a change in the spatial location of one of the items. The results revealed better performance when the items were spread across the two hemifields as compared to when they occupied a single hemifield (Figure 1). Note that the amplitude of the BFA also increased with the number of locations to be remembered (absent with 4 items, $p < 0.01$ with 6 items, and $p<0.005$ with 8 items), supporting the notion that the BFA emerges only when the task is sufficiently complex (Banich & Belger, 1990; Belger & Banich, 1992, 1998; Delvenne et al., 2011a; Merola & Liederman, 1990; Norman et al., 1992; Reuter-Lorenz et al., 1999; Weissman & Banich, 2000; Weisman et al., 2000; Zhang & Feng, 1999).

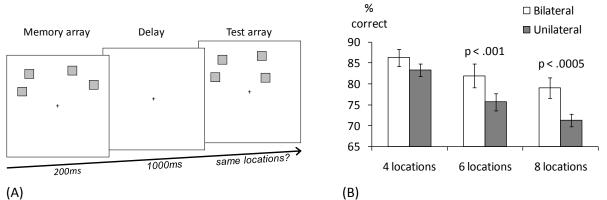(A)   (B)

Fig. 1. (A) Trial sequence (from the bilateral '4 locations' condition) used in the location VSTM study of Delvenne (2005). (B) Results of the experiment. Error bars represent standard errors of the means. (Adapted from Delvenne, 2005.)

The second demonstration of a BFA in VSTM was recently provided by Umemoto and colleagues (2010). The authors used an orientation recall task in which teardrop stimuli or simple lines presented in various orientations were displayed unilaterally or bilaterally for 150 ms. Following a retention interval of 1000 ms, a randomly oriented test stimulus was presented and the task was to adjust its orientation with the computer mouse to match the orientation of the stimulus that occupied the same location in the memory array. The results showed fewer errors in the bilateral condition compared to the unilateral condition (Figure 2), replicated therefore the main results I observed a couple of year ago (Delvenne, 2005). However, the study of Umemoto and colleagues also revealed two additional new findings. Firstly, they demonstrated the existence of a BFA in VSTM even when the stimuli were sequentially presented one at a time within the memory array. This suggests that the BFA in VSTM cannot be, at least exclusively, explained by a difference in the encoding quality between unilaterally and bilaterally presented stimuli. Secondly, using an analytic approach developed by Zhang and Luck (2008)[2], the authors found that the bilateral distribution of information affected the number of items that can be held in VSTM, but not their resolution.

---

[2] In order to provide independent estimates of the number and resolution of the memory representations, Zhang and Luck (2008) used a recall paradigm in which participants had to memorize several colours, and following a brief retention interval, were asked to recall the colour of a probe item by selecting it on a colour wheel. The rational is that if the colour was stored in memory, the selected colour will be near to the original colour. By contrast, if the colour was not stored in memory, the selected colour should be random. The distance between the selected colour and the original one provided some information about the resolution of the memory representations (see Zhang & Luck, 2008, for further details about this approach).
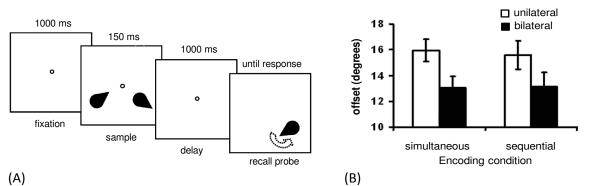
Fig. 2. (A) Trial sequence and (B) results of the spatial orientation VSTM study of Umemoto et al. (2010). Error bars represent 95% confidence interval. (Adapted from Umemoto et al., 2010.)

To sum-up, current findings have revealed a BFA in VSTM when the task involves detecting a location (Delvenne, 2005) or orientation (Gratton et al., 2001; Umemoto et al., 2010) change between two successive visual displays.

3.1.2. Evidence against the Bilateral Field Advantage in Visual Short-Term memory

There are also studies that have failed to find a BFA in VSTM as well as others that have indirectly suggested that the capacity of VSTM does not dependent on the spatial layout of information in the visual field. If the overall capacity of VSTM is the sum of independent capacities in each hemifield, VSTM capacity in one hemifield should be smaller than the overall average capacity in humans, typically estimated at around four items. However, electrophysiological studies that have used the contralateral method (McCollough et al., 2007; Vogel & Machizawa, 2004; Vogel et al., 2005), in which only items in one hemifield had to be stored in memory, have found that the amplitude of the CDA, the electrophysiological marker of VSTM capacity in one hemifield, reached an asymptotic limit at around four items. This limit is similar to the estimated overall average VSTM capacity, indirectly suggesting a similar capacity within and across hemifields.

In the study I conducted in 2005 (Delvenne, 2005), although a BFA was found when the task entailed remembering spatial locations (see previous section), no BFA was observed if the task implied remembering colour information. Specifically, I used a standard change detection task in which a number of coloured squares were briefly presented for 200 ms either within the same hemifield (*unilateral condition*) or split between both hemifields (*bilateral condition*). Following a retention interval of 1000 ms, the colours reappeared and the participants had to detect a change in the colour of one of the items. Performance was found to be similar for unilaterally and bilaterally

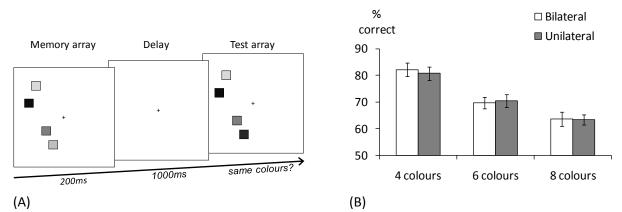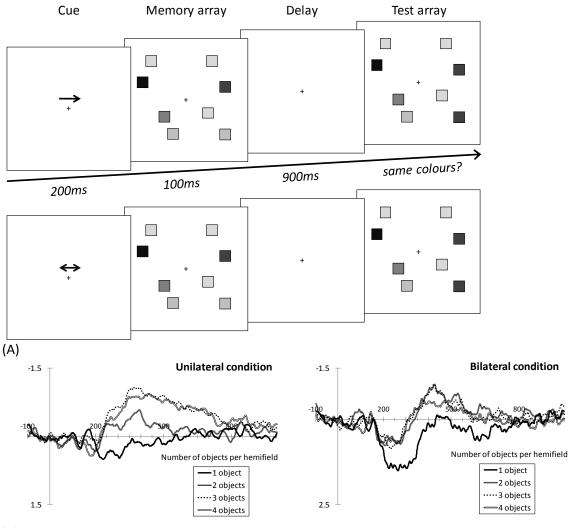presented stimuli, suggesting no BFA for colour VSTM (Figure 3).

Fig. 3. (A) Trial sequence (from the unilateral '4 colours' condition) used in the colour VSTM study of Delvenne (2005). The different grey levels represent different colours. (B) Results of the experiment. Error bars represent standard errors of the means. (Adapted from Delvenne, 2005.)

These findings are supported by two recent change detection studies. Xu and Nakayama (2007) presented participants with two sets of three colours that needed to be encoded and held in memory. The two sets were presented sequentially either in the same single hemifield or one set on the left hemifield and one set on the right hemifield. Xu and Nakayama observed no difference in change detection performance between those two conditions. Likewise, Mance and colleagues (Mance, Becker, & Liu, 2011) asked participants to encode and maintain two colours that appeared either within the same hemifield or in opposite hemifields. The two colours appeared also either simultaneously or sequentially. Again, the results revealed no BFA, be it in the simultaneous or sequential mode of presentation.

It may be argued that the change detection paradigm may not be totally appropriate and sensitive enough to reveal a BFA as it is not a direct measure of VSTM capacity. Since a comparison process between a visual input (i.e., the test array) and a memory representation (i.e., the memory array) is required in a change detection task, performance reflects what remains available in memory after the onset of the test array and during the comparison process. For example, it has been shown that a failure in the comparison process can occur despite the successful encoding and storage of the to-be-compared item (Mitroff, Simons, & Levin, 2004). As a result, the change detection paradigm may lead to underestimation of the maximum number of items that can actually be held in VSTM (Awh, Barton, & Vogel, 2007; Delvenne, Cleeremans, & Laloyaux, 2010; Hollingsworth, 2003; Landman, Spekreijse, & Lamme, 2003). It is therefore possible that this paradigm obscures the effects of the bilateral presentation. This speculation falls in line with the findings from Umemoto and colleagues (2010) showing a consistent BFA for orientation information using recall procedures, namely when the test array and the comparison process stage were removed from the task, but less constant BFA for the same stimuli when using the change detection paradigm.

However, evidence suggests that the failure to find a BFA in the colour memory task (Delvenne, 2005) cannot be explained by the lack of sensibility of the change detection paradigm. Firstly, Umemoto and colleagues (2010) reported having found no BFA with colour information, even in a recall paradigm (p. 78). Secondly, we recently provided evidence for the absence of a BFA in colour VSTM in an electrophysiological study (Delvenne et al., 2011b). The great benefit of using electrophysiological measures is that it allows us to track the on-line maintenance of visual information in memory, prior the onset of the test array. Here, the dependent variable was not the change detection accuracy, but rather the amplitude of the CDA during memory maintenance.

Participants were required to maintain multiple colours either from one hemifield (unilateral condition) or from both hemifields (bilateral condition). Consistent with previous research (McCollough et al., 2007; Vogel & Machizawa, 2004), the CDA amplitude increased as function of set size but ceased getting larger for arrays of four colours in the unilateral condition. In the bilateral condition, however, this contralateral activity already reached its asymptotic limit for arrays of two colours per side (i.e., four colours across both hemifields) (Figure 4). This shows that despite the contralateral nature of the CDA, this activity is modulated by the overall number of items presented in both hemifields, supporting the notion that VSTM capacity is insensitive to the spatial distribution of information across hemifields.

Fig. 4. (A) Trial sequences (from the unilateral and bilateral '4 objects' conditions) used in the EEG study of Delvenne et al. (2011b). The different grey levels represent different colours. (B) CDAs (ipsilateral activity subtracted from contralateral activity) at posterior electrode sites for arrays of one, two, three, and four objects per hemifield obtained in the unilateral and bilateral conditions. (Adapted from Delvenne et al., 2011b.)

The absence of a BFA in VSTM is also supported, although indirectly, by the neuropsychological investigation carried out by Duncan and colleagues in patients with unilateral (right) parietal lobe lesions and showing signs of spatial neglect (Duncan, Bundesen, Olson, Humphreys, Chavda, & Shibuya, 1999). The patients were asked to report letters (one to five) that briefly appeared in the

11

left or right visual field. If independent capacities exist in the left and right hemispheres for VSTM, one might expect performance in those patients to be impaired when the to-be-remembered items are presented to the contralateral side of the lesion (i.e., the left hemifield), but not when the items are presented to the ipsilateral side (i.e., the right hemifield). Against this hypothesis, the results revealed that VSTM capacity was equally impaired on the two sides in those patients.

In summary, current evidence have revealed the absence of a BFA in VSTM when the task involves detecting a colour change between two successive visual displays (Delvenne, 2005; Delvenne et al., 2011b; Mance et al., 2011; Umemoto et al., 2011; Xu & Nakayama, 2007) or when it implies reporting previously presented letters (Duncan et al, 1999).

3.2. Review of possible accounts

3.2.1. Task complexity

Why have past studies yielded inconsistent evidence for a BFA in VSTM? Although clearly further research is needed to fully understand the BFA and its effect on memory, one possibility is that the BFA is contingent on task complexity. Indeed, past research using non-mnemonic visual tasks, such as matching (Banich & Belger, 1990; Belger & Banich, 1992, 1998; Merola & Liederman, 1990; Norman et al., 1992; Reuter-Lorenz et al., 1999; Weissman & Banich, 2000; Weisman et al., 2000; Zhang & Feng, 1999) or enumerating visual items (Delvenne et al., 2011a) for instance, has shown that the BFA happens to emerge only when the task is sufficiently complex and attentionally demanding Albeit the memory studies reviewed here seem rather alike in terms of task and procedure that they used (i.e., they mainly used the change detection paradigm), none of them were exactly similar and some tasks may have been logically more complex than others. It is therefore sensible to examine whether the inconsistency in finding a BFA in VSTM could be explain by a difference in the complexity of the tasks used in those studies.

The complexity undeniably plays an important role on the emergence of the BFA. If the task is too easy – and this applies for any sorts of task, not only memory tasks – it will be difficult to find some factors that can increase the level of already-high performance. To observe a benefit of splitting the information between both hemifields, performance should not be already at ceiling or nearly flawless when information is presented in only one hemifield. The need of a minimum of complexity can be witnessed in Delvenne (2005)'s study, for example, in which the BFA in the spatial location short-term memory task occurred only in the most complex conditions. In particular, the BFA was observed in larger set sizes (i.e., when four or six locations had to be remembered), but not in the smallest set size (i.e., when two locations had to be held in memory) (see Figure 1).

However, a closer examination of the performance across experiments and studies does not seem to suggest a direct cause-effect relationship between task complexity and the emergence of the BFA in VSTM. For example, in Delvenne (2005)'s study, the same participants performed both the spatial and colour short-term memory tasks. In average, performance was the lowest in the colour memory task, suggesting that this task was more complex than the spatial task. Nonetheless, the BFA was only observed in the spatial memory task (i.e., the less difficult task), and not in the colour memory task. Thus, although the memory task must be sufficiently complex for a BFA to emerge, complexity itself cannot explain the inconsistency of past research, nor forecast whether or not a BFA will occur.

3.2.2. Spatial/object short-term memory dissociation

The most obvious disparity that can be found between studies that have revealed a BFA in VSTM and those that have not is the type of information that participants were required to encode and hold in memory. Studies that have found a BFA in VSTM had examined memory for spatial information, particularly spatial locations (Delvenne, 2005) and orientations (Gratton et al., 2001; Umemoto et al., 2010). By contrast, studies that have failed to observe it had examined memory for identity information, in particular colour information (Delvenne, 2005; Delvenne et al., 2011b; Mance et al., 2011; Umemoto et al., 2011; Xu & Nakayama, 2007) and letters (Duncan et al, 1999). In view of this distinction, one possibility is that the spatial distribution of visual inputs in the left and right visual fields affects memory for spatial information, and not memory for object identity.

In vision, it is widely acknowledged that processing the location of an object requires some distinct brain regions from those involved in processing the identity of the object (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). Spatial locations is processed in the occipito-parietal regions (also known as the "dorsal stream" or "where pathway") and object identification involves the occipito-temporal regions ("ventral stream" or "what pathway"). A number of behavioural (Darling, Della Sala, & Logie, 2009; Tresch, Sinnamon, & Seamon, 1993; Woodman & Luck, 2004; Woodman, Vogel, & Luck, 2001), neuropsychological (Darling, Della Sala, Logie, & Cantagallo, 2006; Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999; De Renzi & Nichelli, 1975; Hanley, Young, & Person, 1991) and neuroimaging studies (Courtney, Ungerleider, Keil, & Haxby, 1996; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Fuster & Jervey, 1981; McCarthy, Puce, Constable, Krystal, Gore, & Goldman-Rakic, 1996; Smith & Jonides, 1997; Ungerleider, Courtney, & Haxby, 1998; Ventre-Dominey, Bailly, Lavenne, LeBars, Mollion, Costes, & Dominey, 2005; Xu, 2009; Xu & Chun, 2006) have suggested that the division between spatial and object processing extends to short-term memory. For example, using positron emission tomography (PET), Ventre-Dominey and colleagues (2005) found that a spatial short-term memory (STM) tasks activated dorsal circuits mainly in the occipito-parietal cortex and the dorsal region of the prefrontal cortex, whereas the object STM tasks recruited ventral circuits in the occipito-temporal regions, the ventral area of the prefrontal cortex, and the striatum.

The idea that the bilateral field presentation of visual inputs affects memory for dorsal stream visual properties, but not memory for ventral stream visual properties, implies that the contralateral organisation of the visual system extends to the parietal cortex, but not to the temporal cortex. In support to this assumption, it has been shown that the parietal cortex, including the intra-parietal sulcus (IPS), contains a map of retinotopically-coded neurons that represent spatial locations (Kusonoki & Goldberg, 2003; Sereno, Pitzalis, & Martinez, 2001). In addition, damage to the left or right parietal lobe can result in denying awareness of information in the contralateral visual field, a syndrome known as *unilateral neglect* (Brain, 1941). Furthermore, although recent electrophysiological studies have demonstrated the existence of the contralateral organization of visual memories by revealing the CDA (McCollough et al., 2007; Vogel & Machizawa, 2004), the potential candidate source localization of this activity has been proposed to be the parietal cortex, in particular the intra-parietal sulcus (IPS). Indeed, like the CDA, the neural activity in the IPS has been found to be strongly modulated by the number of items held in memory and to reach also an asymptotic limit of approximately 4 items (Todd & Marois, 2004; Xu, 2009; Xu & Chun, 2006). The dorsal scalp topography of the CDA suggests that the contralateral organization of visual memories finds its source in the parietal cortex, mainly involved in spatial processing. By contrast, the preservation of the contralateral organisation in the temporal cortex is less clear. Some data seem to suggest that such organisation is retained in the inferior regions of the temporal cortex (Chelazzi, Miller, Duncan, & Desimone, 1993) while neuropsychological data suggest that the temporal cortex represents information from both sides. For instance, damage to either temporal lobe can result in difficulty in identifying and recognizing visual objects presented to either hemifield, a syndrome called *agnosia* (Lissauer, 1890).

If processing spatial information is, to some extent, independent in the left and right hemifields, it is plausible to suggest that the bilateral field presentation of visual information would benefit spatial processing, including spatial STM. By contrast, if processing non-spatial object information in one hemifield involves neural activity in both temporal lobes, one may assume that the bilateral field presentation of visual information would not benefit object processing, including object STM. In support to this, and as mentioned in previous sections, the clearest and strongest BFA found in a high-level visual task was demonstrated in a MOT task, in which spatial locations needed to be continually monitored (Alvarez & Cavanagh, 2005). MOT and spatial STM are closely related as they both recruit dorsal circuits. Importantly, spatial STM but not visual STM has been found to be impaired by a concurrent MOT task (Zhang, Xuan, Fu, & Pylyshyn, 2010). Together, those findings suggest that the source of the BFA in VSTM might be spatial processing.

3.2.3. Attentional selection

Although the spatial/object processing dissociation account appears to be a good candidate to explain the BFA in VSTM, it might encounter some difficulties at explaining a number of past BFA demonstrations in visual non-mnemonic tasks. Specifically, if the BFA is a signature of spatial processing, how can this effect occur in tasks involving the identification of targets (Awh & Pashler, 2000; Chakravarthi & Cavanagh, 2006; Reardon et al., 2009; Scalf et al., 2007) or the search for a target in a visual display (Alvarez & Cavanagh, 2006)? Because those tasks are dominated by the identification process rather than by spatial processing, they should not exhibit a BFA according to the spatial/object processing dissociation account. A close examination of those studies reveals that the BFA emerged only when the targets had to be selected to the exclusion of distracters. By contrast, the BFA failed to emerge in the absence of distracters. For example, in Reardon and colleagues (2009)'s study, participants were required to detect peripheral Gabor targets with Gabor distracters present in half of the trials. The stimuli were either presented in one hemifield or divided across the left and right hemifield. Detection performance exhibited a BFA only when distracters were present, thus when attentional requirements were high.

If the process of attentional selection is particularly sensitive to bilateral presentations, would we then observe a BFA in an object STM task provided that the to-be-remembered objects had to be selected to the exclusion of distracters? The answer seems to be "yes". We have recently examined this idea in a colour change detection task (Holt & Delvenne, *submitted for publication*). We contrasted three conditions: in the *2 targets* and *4 targets conditions*, two and four coloured circles were presented, respectively, whereas in the *distracters condition*, two coloured circles together with two coloured crosses were displayed. The stimuli were presented either bilaterally or unilaterally, and all those conditions were randomly mixed. Participants were asked to ignore the colours of the crosses and to make their change detection judgment on the colours of the circles only. The results revealed a BFA in the *distracters condition* only, indicating a major role of attentional selection in the emergence of the BFA (Figure 5). Those findings also suggest that it is not the nature of the to-be-remembered features (i.e., spatial/object) per se that determines whether a BFA would emerge.
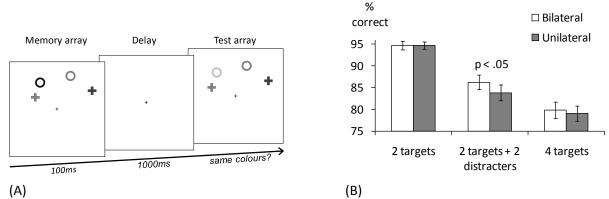
Fig. 5. (A) Trial sequence (from the bilateral, distracter condition) used in the study of Holt and Delvenne (*submitted for publication*). The different grey levels represent different colours. (B) Results of the experiment. Error bars represent standard errors of the means. (Adapted from Holt & Delvenne, *submitted for publication*).

If attentional selection is the source of the BFA, why does spatial STM show a BFA even when no distracters are present in the visual display (Delvenne, 2005; Gratton et al., 2001; Umemoto et al., 2010)? Although no definitive explanation can be given at present, one possibility is that, by definition, a spatial STM task is already dominated by the attentional selection stage. This hypothesis makes sense if we assume that VSTM is a sequence of capacity-limited processes, beginning with the selection of the to-be-remembered objects through their spatial locations (i.e., object individuation – Xu & Chun, 2006) and then proceeding to higher-level operations such as the encoding of objects details (i.e., object identification – Xu & Chun, 2006), and finally the maintenance in memory (i.e., object storage). For example, using the functional Magnetic Resonance Imaging (fMRI) technique, Xu and colleagues (Xu, 2009; Xu & Chun, 2006) have recently provided clear evidence for separate neural mechanisms underlying object individuation and object identification. Specifically, Xu and colleagues found that the inferior intra-parietal sulcus (IPS) selects a fixed number of approximately four objects via their spatial locations (object individuation) and the superior IPS and the lateral occipital complex (LOC) process a subset of the objects selected and encode their detailed visual properties (object identification). Perhaps, the bilateral field presentation of visual inputs affects the object individuation process rather than the object identification process. As Xu and Chun (2006) suggested, the selection of information by object individuation mechanisms may not only determine which objects can be held in VSTM, but also which ones can be enumerated or attentionally tracked. Evidence for a BFA in both visual enumeration (Delvenne et al., 2011a) and object tracking (Alvarez & Cavanagh, 2005) strongly supports the idea that the BFA takes its source at the object individuation stage.

Furthermore, because the objects need to be selected before they can be identified, the object individuation-identification theory suggests that object individuation precedes object identification. This asymmetry between spatial processing and object processing is also supported by Jiang and colleagues (2000), who found in a change detection study that altering the shape or colour of the items had no effects on memory for their locations, whereas changing the location of the items affected memory for their colour or shape. In that context, we may assume that spatial STM mainly involves two stages. Firstly, the objects are selected via their spatial locations (object individuation). Secondly, those locations are held in memory (object storage). Because there is no need to encode the detailed properties of the objects (object identification) in a spatial STM task, it is plausible to suggest that such a task is dominated by the object individuation stage, in which the attentional selection process plays a major role. If the BFA is a signature of attentional selection, then there is a

15

great chance this effect will emerge in a spatial STM task, as shown in recent studies (Delvenne, 2005; Gratton et al., 2001; Umemoto et al., 2010). By contrast, an object STM task requires the additional stage of object individuation. First, the objects are selected (object individuation), then their detailed visual properties are processed and encoded (object identification), and finally those object details are maintained in memory (object storage). An object STM task may be particularly dominated by the object identification stage since this stage is subsequent to the object individuation stage. This may result in obscuring the initial BFA, as demonstrated in previous studies (Delvenne, 2005; Delvenne et al., 2011b; Mance et al., 2011; Umemoto et al., 2010; Xu & Nakayama, 2007). As shown by our recent findings (Holt & Delvenne, *submitted for publication*), a BFA can emerge in an object STM task, but only when the demand of attentional resources onto the object individuation stage is particularly high (e.g., by placing targets amongst distracters).

The process of target selection is not limited to the encoding stage but can also operate within memory representations. A large body of recent research has found that once objects are transferred into VSTM, they can still be selectively accessed by attentional mechanisms (Delvenne et al., 2010; Griffin & Nobre, 2003; Landman et al., 2003; Makovski & Jiang, 2007; Makovski, Sussman, & Jiang, 2008; Matsukura, Luck, & Vecera, 2007; Nobre, Coull, Maquet, Frith, Vandenberghe, & Mesulam, 2004). Those studies used the retro-cuing paradigm, in which an attentional spatial cue (e.g., an arrow) that pointed to the location previously occupied by an object was presented during the retention interval of the memory task. It was found that memory for the cued object was significantly better than memory for the uncued objects. Importantly, the process of selecting a subset of objects held in memory appears to also exhibit a BFA. In a retro-cuing study, we have recently observed that selecting two memory objects that were presented in separate hemifields within the memory array is more efficient than selecting two objects from within the same hemifield (Delvenne & Holt, *submitted for publication*). Such a benefit of splitting attention across the two sides of internal representations may account for the BFA observed when the items were sequentially presented within the memory array (Gratton et al., 2001; Umemoto et al., 2010). In a sequential presentation, the selection of information at the encoding stage is controlled in that all the items are selected in the same way, be it in a bilateral or unilateral condition. But because attention can still operate beyond the phase of perceptual encoding, namely on internal representations, the BFA in a sequential presentation may still reflect the better ability to split attentional selection mechanisms across both hemifields as compared to within a single one.

4. Conclusion

The study of VSTM has become a very active area of research over the past 15 years and has largely focused on its storage capacity. Albeit highly limited, the capacity of this system has been found to be modulated by a number of factors, such as object complexity (Alvarez & Cavanagh, 2004), the nature of the features (Delvenne & Bruyer, 2004) or perceptual integration (Luck & Vogel, 1997), among others. Determining what may influence the number of visual objects that can be simultaneously held in memory is crucial as it may help us to develop ways to improve VSTM capacity, and thus daily behavioural performance that depends on it (Xu & Nakayama, 2007).

This chapter was focused on a newly discovered factor, namely the spatial distribution of the to-be-remembered objects across the left and right visual fields. Despite few published reports, current data seem to suggest that the capacity of VSTM can benefit from the division of visual inputs across both hemifields, thanks to independent (or at least semi-independent) attentional resources in the left and right hemifields. A BFA can therefore be observed in VSTM when the task is dominated by the spatial selective attention stage, such as VSTM for spatial information (Delvenne, 2005; Gratton

et al., 2001; Umemoto et al., 2010) or VSTM for a subset of targets that have to be selected to the exclusion of distracters (Holt & Delvenne, *submitted for publication*).

More research is needed to elucidate the source of the BFA in VSTM. Nonetheless, in view of these recent discoveries, it is clear that to further understand VSTM, it will be critical to take into account the existence of the contralateral organisation of the visual space at early stages of visual processing and the possible existence of independent attentional resources in the left and right hemifields. If determining the factors that influence VSTM capacity may be essential to understand why VTSM is limited in the first place, understanding the BFA may be critical to answering an even broader question about the human brain, specifically why it is divided into two cerebral hemispheres.

5. References

Alvarez, G. A. & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science, 15*, 106–111.

Alvarez, G. A, & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifield. *Psychological Science, 16*, 637–643.

Alvarez, G. A. & Cavanagh, P. (2006). Hemifield independence is a signature of location-based attentional filtering. *Journal of Vision*, *6*(6), 943a.

Awh, E., Barton, B., Vogel, E. K. (2007). Visual working memory represents a fixed number of items, regardless of complexity. *Psychological Science, 18(7)*, 622-628.

Awh, E. & Jonides, J. (2001). Overlapping mechanisms of attention and working memory. *Trends in Cognitive Sciences, 5(3)*, 119-126.

Awh, E. & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance, 26*, 834–846.

Awh, E., Smith, E. E., & Jonides, J. (1995). Human rehearsal processes and the frontal lobes: PET evidence. In J. Grafman, K. Holyoak, & F. Boller (Eds.) *Structure and functions of the human prefrontal cortex Annals of the New York Academy of Sciences., vol. 769*, 97-119. New York, NY:, New York Academy of Sciences.

Baddeley, A. D. & Hitch, G. J. (1974). Working memory. In G.A. Bower (ed.), *Recent Advances in Learning and Motivation*, Vol. 8 (pp. 47–89). New York: Academic Press.

Baird, L. M. & Burton, A. M. (2008). The bilateral advantage for famous faces: Interhemispheric communication or competition? *Neuropsychologia, 46(5),* 1581-1587.

Banich, M. T. & Belger, A. (1990). Interhemispheric interaction: How do the hemispheres divide and conquer a task? *Cortex, 26*, 77-94.

Belger, A. & Banich, M. T. (1992). Interhemispheric interactions affected by computational complexity. *Neuropsychologia, 30*, 923-929.

Belger, A. & Banich, M. T. (1998). Costs and benefits of integrating information between the hemispheres: a computational perspective. *Neuropsychology, 12,* 380-398.

Berger, J. M. (1988). Interhemispheric cooperation and activation in integration of verbal information. *Behavioural Brain Research, 29*, 193-200.

Brady, T. F., Konkle, T., & Alvarez, G. A. (2011). A review of visual memory capacity: Beyond individual items and toward structured representations. *Journal of Vision, 11(5)*, 1-4.

Brain, R. W. (1941). Visual disorientation with special reference to lesion of the right brain hemisphere. *Brain, 64,* 244-272.

Brown, W. S., Jeeves, M. A., Dietrich, R., & Burnison, D. S. (1999). Bilateral field advantage and evoked potential interhemispheric transmission in commissurotomy and callosal agenesis. *Neuropsychologia, 37*, 1154-1180.

Bullier, J. (2004). Communications between cortical areas of the visual system. In L.M. Chalupa & J.S. Werner (Eds.), *The visual neurosciences* (pp. 522–540). Cambridge, MA: MIT Press.

Butcher, S. & Cavanagh, P. (2008). Unilateral field advantage for detecting repeated elements. *Perception & Psychophysics, 70*, 714-724.

Castiello, U., & Umilta, C. (1992). Splitting focal attention. *Journal of Experimental Psychology: Human Perception and Performance, 18(3)*, 837–848.

Chakravarthi, R. & Cavanagh, P. (2009). Bilateral field advantage in visual crowding. *Vision Research, 49*, 1638-1646.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal (IT) cortex. *Nature, 363*, 345-347.

Chiang, T. C., Walsh, V., & Lavidor, M. (2004). The cortical representation of foveal stimuli: evidence from quadrantanopia and TMS-induced suppression. *Brain Research. Cognitive Brain Research*, *21*, 309–316.

Collin, C. A., McMullen, P. A., & Seguin, J.-A. (2009). A significant bilateral field advantage for shapes defined by static and motion cues. *Perception, 38*, 1132-1143.

Compton, R. J. (2002). Inter-hemispheric interaction facilitates face processing. *Neuropsychologia, 40*, 2409–2419.

Courtney, S. M., Petit, L., Maisog, J. M., Ungerleider, L. G., & Haxby, J. V. (1998). An area specialized for spatial working memory in human frontal cortex. *Science, 279,* 1347–1351.

Courtney, S. M., Ungerleider, L. M., Keil, K., & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex, 6*, 39–49.

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences, 24*, 87-114.

Culham, J., Cavanagh, P., & Kanwisher, N. (2001). Attention Response Functions: Characterizing Brain Areas Using fMRI Activation during Parametric Variations of Attentional Load. *Neuron, 32,* 737-745.

Curby, K. M., Glazek, K., & Gauthier. I. (2009). A visual short-term memory advantage for objects of expertise. *Journal of Experimental Psychology: Human Perception & Performance, 35*, 94 - 107.

Darling, S., Della Sala, S., Logie, R.H. (2009). Dissociation between appearance and location within visuo-spatial working memory. *Quarterly Journal of Experimental Psychology, 62,* 417-425*.*

Darling, S., Della Sala, S., Logie, R. H., & Cantagallo, A. (2006). Neuropsychological evidence for separating components of visuo-spatial working memory. *Journal of Neurology, 253*, 176–180.

Davis, R. & Schmit, V. (1971). Timing the transfer of information between the hemispheres in man. *Acta Psychologica, 36*, 335-346.

Della Sala, S., Gray, C., Baddeley, A. D., Allamano, N., & Wilson, L. (1999). Pattern span: A tool for unwelding visuo-spatial memory. *Neuropsychologia, 37*, 1189–1199.

Delvenne, J.-F. (2005). The capacity of visual short-term memory within and between hemifields. Cognition, 96, B79–B88.

Delvenne, J.-F., Braithwaite, J. J., Riddoch, M. J., & Humphreys, G. W. (2002). Capacity limits in Visual Short-Term Memory for local orientations. *Current Psychology of Cognition, 21(6),* 681-690.

Delvenne, J.-F. & Bruyer, R. (2004). Does visual short-term memory store bound features? *Visual Cognition, 11(1)*, 1-27.

Delvenne, J.-F. & Bruyer, R. (2006). A configural effect in visual short-term memory for features from different parts of an object. *The Quarterly Journal of Experimental Psychology, 59(9)*, 1567-1580.

Delvenne, J.-F., Castronovo, J., Demeyere, N., & Humphreys, G. W. (2011a). Bilateral field advantage in visual enumeration. *PLoSONE 6(3)*: e17743.

Delvenne, J.-F., Cleeremans, A., & Laloyaux, C. (2010). Feature bindings are maintained in visual short-term memory without sustained focused attention. *Experimental Psychology, 57(2)*, 108-116.

Delvenne, J.-F. & Holt, J. L. (*submitted for publication*). Splitting attention across the two visual fields in visual short-term memory.

Delvenne, J.-F., Kaddour, L., & Castronovo, J. (2011b). An electrophysiological measure of visual short-term memory capacity within and across hemispheres. *Psychophysiology, 48*, 333-336.

De Renzi, E. & Nichelli, P. (1975). Verbal and non-verbal short-term memory impairment following hemispheric damage. *Cortex*, *11*, 341-354.

Dimond, S. J. & Beaumont, J. G. (1971). Use of two cerebral hemispheres to increase brain capacity. *Nature, 232*, 270-271.

Dimond, S. J. & Beaumont, J. G. (1972). Processing in perceptual integration between and within the cerebral hemispheres. *British Journal of Psychology, 63(4)*, 509-517.

Drew, T. & Vogel, E. K. (2008). Neural measures of individual differences in selecting and tracking multiple moving objects. *Journal of Neuroscience, 28*, 4183–4191.

Duncan, J., Bundesen, C., Olson, A., Humphreys, G. W., Chavda, S., & Shibuya, H. (1999). Systematic analysis of deficits in visual attention. *Journal of Experimental Psychology: General, 128*, 450–478.

Eimer, M. & Kiss, M. (2010). An electrophysiological measure of access to representations in visual working memory. *Psychophysiology, 47*, 197-200.

Eviatar, Z. & Zaidel, E. (1994). Letter matching within and between the disconnected hemispheres. *Brain and Cognition, 25*, 128-137.

Fougnie, D. & Marois, R. (2006). Distinct capacity limits for attention and working memory: Evidence from attentive tracking and visual working memory paradigms. *Psychological Science, 17*(6), 526-534.

Fuster, J. M. & Jervey, J. P. (1981). Inferotemporal neurons distinguish and retain behaviorally relevant features of visual stimuli. *Science, 212,* 952-955.

Gazzaniga, M. S. & Young, E. D. (1967). Effects of commissurotomy on the processing of visual information. *Experimental Brain Research, 3*, 368-371.

Goodale, M. A. & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience, 15*(1), 20-25.

Gratton, G. (1998). The contralateral organization of visual memory: A theoretical concept and a research tool. *Psychophysiology, 35*, 638-647.

Gratton, G., Corballis, P. M., & Jain, S. (1997). Hemispheric organization of visual memories. *Journal of Cognitive Neuroscience, 9*, 92-104.

Gratton, G., Fabiani, M., & Corballis, P. M. (2001).Working memory capacity and the hemispheric organization of the brain: A commentary to Cowan, 2001. *Behavioral and Brain Sciences, 24(1)*, 121-122.

Griffin, I. C. & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience, 15*, 1176-1194.

Hanley, J. R., Young, A. W., & Pearson, N. A. (1991). Impairment of the visuo-spatial sketch pad. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 43A(1),* 101-125.

Harrison, S. A. & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature, 458*, 632–635.

Hatta, T. & Tuji, S. (1993). Interhemispheric integration of number stimuli: comparison of Arabic with kanji numerals. *Cortex, 29*, 359–364.

Hayes, M. T., Swallow, K. M., & Jiang, Y. V. (2010). The unilateral field advantage in repetition detection: Effects of perceptual grouping and task demands. *Attention, Perception, & Psychophysics*, *72 (3),* 583-590.

Hollingworth, A. (2003). Failures of retrieval and comparison constrain change detection in natural scenes. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 388-403.

Holt, J. L., & Delvenne, J.-F. (*Submitted for publication)*. A bilateral field advantage in controlling access to visual short-term memory.

Holtzman, J. D. & Gazzaniga, M. S. (1985). Enhanced dual task performance following callosal commissurotomy in humans. *Neuropsychologia, 23*, 315-321.

Jackson, M. C. & Raymond, J. E. (2008). Familiarity enhances visual working memory for faces. *Journal of Experimental Psychology: Human Perception & Performance, 34*(3), 556-568.

Jiang, Y., Olson, I. R., & Chun, M. M. (2000). Organization of visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *26*, 683-702.

Jolicoeur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006a). Attentional control and capture in the attentional blink paradigm: Evidence from human electrophysiology. *European Journal of Cognitive Psychology, 18*, 560–578.

Jolicoeur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006b). On the control of visual spatial attention: Evidence from human electrophysiology. *Psychological Research, 70*, 414–424.

Klingberg, T., O'Sullivan, B. T., & Roland, P. E. (1997). Bilateral activation of fronto-parietal networks by incrementing demand in a working memory task. *Cerebral Cortex, 7,* 465–471.

Klaver, P., Talsma, D., Wijers, A. A., Heinze, H. J., & Mulder, G. (1999). An event-related brain potential correlate of visual short-term memory. *Neuroreport, 10*, 2001–2005.

Koivisto, M. (2000). Interhemispheric interaction in semantic categorization of pictures. *Cognitive Brain Research, 9*, 45-51.

Kraft, A., Muller, N. G., Hagendorf, H., Schira, M. M., Dick, S., Fendrich, R. M., & Brandt, S. A. (2005). Interactions between task difficulty and hemispheric distribution of attended locations: Implications for the splitting attention debate. *Cognitive Brain Research, 24(1),* 19–32.

Kraft, A., Pape, N., Hagendorf, H., Schmidt, S., Naito, A., & Brandt, S. A. (2007). What determines sustained visual attention? The impact of distracter positions, task difficulty and visual fields compared. *Brain Research, 1133(1),* 123–135.

Kusonoki, M. & Goldberg, M. E. (2003). The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. *Journal of Neurophysiolo021010y, 89(3)*, 1519-27.

Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity of storage of integrated objects before change blindness. *Vision Research, 43*, 149-164.

Langham, M., Hole, G., Edwards, J., & O'Neill, C. (2002). An analysis of 'looked but failed to see' accidents involving parked police cars. *Ergonomics, 45*, 167–185.

Lavidor, M. & Walsh, V. (2004). The nature of foveal representation. *Nature Reviews Neuroscience*, *5*, 729–735.

Liederman, J., Merola, J. & Martinez, S. (1985). Interhemispheric Collaboration in Response to Simultaneous Bilateral Input. *Neuropsychologia, 23,* 673-683.

Lissauer, H. (1890). Ein Fall von Seelenblindheit nebst einem beitrage zur Theorie derselben. *Archiv für Psychiatrie und Nervenkrankheiten*, *21*, 22–270. English translation by Jackson, M. (1988). Lissauer on agnosia. *Cognitive Neuropsychology*, *5*, 155–192.

Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1989). Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature, 342*, 543–545.

Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1994). Independent attentional scanning in the separated hemispheres of split-brain patients. *Journal of Cognitive Neuroscience*, *6*, 84-91.

Luck, S. J. & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279–281.

Ludwig, T. E., Jeeves, M. A., Norman, W. D., & DeWitt, R. (1993). The bilateral field advantage on a letter-matching task. *Cortex, 29*, 691-713.

Makovski, T. & Jiang Y. V. (2007). Distributing versus focusing attention in visual short-term memory. *Psychonomic Bulletin & Review, 14(6),* 1072-1078.

Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 34(2),* 369-380.

Mance, I., Becker, M. W., & Liu, T (2011, May 30). Parallel consolidation of simple features into visual short-term memory. *Journal of Experimental Psychology: Human Perception & Performance.* Advance online publication. doi: 10.1037/a0023925.

Mason, C. & Kandel, E. R. (1991). Central visual pathways. In E. R. Kandel, J. H. Schwarz, & T. M. Jessell (Eds.), *Principles of neural science* (3rd ed., pp. 420–439). Norwalk, Connecticut: Appleton & Lange.

Matsukura, M., Luck, S. J., & Vecera, S. P. (2007). Attention effects during visual short-term memory maintenance: Protection or prioritization? *Perception & Psychophysics, 69*, 1422-1434.

McCarthy, G., Puce, A., Constable, R. T., Krystal, J. H., Gore, J. C., & Goldman-Rakic, P. (1996). Activation of human prefrontal cortex during spatial and nonspatial working memory tasks measured by functional MRI. *Cerebral Cortex, 6,* 600–611.

McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex, 43*(1), 77-94.

Merola, J. L. & Liederman, J. (1990). The effect of task difficulty upon the extent to which performance benefits from between-hemisphere division of inputs. *International Journal of Neuroscience, 51,* 35–44.

Miller, E. K, Erickson, C. A, Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience, 16*, 5154 –5167.

Miniussi, C., Girelli, M., & Marzi, C. A. (1998). Neural site of the redundant target effect: electrophysiological evidence. *Journal of Cognitive Neuroscience, 10*, 2, 216-230.

Mitroff, S. R., Simons, D. J., & Levin, D. T. (2004). Nothing compares 2 views: Change blindness can occur despite preserved access to the changed information. *Perception & Psychophysics, 66,* 1268-1281.

Muller, M. M., Malinowski, P., Gruber, T., & Hillyard, S. A. (2003). Sustained division of the attentional spotlight. *Nature, 424*, 309–312.

Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., & Mesulam, M. M. (2004). Orienting Attention to Locations in Perceptual Versus Mental Representations. *Journal of Cognitive Neuroscience, 16,* 363-373.

Norman, W. D., Jeeves, M. A., Milne, A., & Ludwig, T. E. (1992). Hemispheric interactions: The bilateral advantage and task difficulty. *Cortex* , *28* , 623-642.

Oksama, L. & Hyönä, J. (2004). Is multiple object tracking carried out automatically by an early vision mechanism independent of higher order cognition? An individual difference approach. *Visual Cognition, 11*, 631–671.

Olson, I. R. & Jiang, Y. (2002). Is visual short-term memory object based? Rejection of the "strong-object" hypothesis. *Perception & Psychophysics, 64*, 1055–1067.

Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, *44*, 369-378.

Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics*, *16*, 283-290.

Pollman, S., Zaidel, E., & von Cramon, D. Y. (2003). The neural basis of the bilateral distribution advantage. *Experimental Brain Research, 221,* 322–333.

Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*, 23-38.

Pylyshyn, Z. W. & Storm, R. W. (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spatial Vision, 3(3*), 1-19.

Reardon, K. M., Kelly, J. G., & Matthews, N. (2009). Bilateral Attentional Advantage on Elementary Visual Tasks. *Vision Research, 49(7)*, 692-702.

Rensink, R. A., O'Regan, J. K., & Clark, J. J. (1997). To see or not to see: The need for attention to perceive changes in scenes. *Psychological Science, 8*, 368–373.

Reuter-Lorenz, P. A., Stanczak, L., & Miller, A. (1999). Neural recruitment and cognitive aging: Two hemispheres are better than one especially as you age. *Psychological Science 10*, 494-500.

Scalf, P., Banich, M. T., Kramer, A. F., Narechania, K., & Simon, C. D. (2007). Double take: Parallel processing by the cerebral hemispheres reduces the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance, 33*, 298–329.

Serences, J., Ester, E., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychological Science, 20(2)*, 207-214.

Sereno, A. B. & Kosslyn, S. M. (1991). Discrimination within and between hemifields: A new constraint on theories of attention. *Neuropsychologia, 29*, 659-675.

Sereno, M. I., Pitzalis, S., & Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science, 294,* 1350-1354.

Simons, D. J. & Levin, D. T. (1997). Change Blindness. *Trends in Cognitive Science, 1*, 261–267.

Simons, D. J. & Levin, D. T. (1998). Failure to detect changes to people in a real-world interaction. *Psychonomic Bulletin and Review, 5(4),* 644–649.

Smith, E. E. & Jonides, J. (1997). Working memory: A view from neuroimaging. *Cognitive Psychology*, *33*, 5-42.

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General & Applied*, *74*, 1-29.

Supèr, H., Spekreijse, H., & Lamme, V. A. F. (2001). A neural correlate of working memory in the monkey primary visual cortex. *Science, 293,* 120 –124.

Todd, J. J. & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature, 428*, 751-754.

Todd, J. J. & Marois, R. (2005). Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. *Cognitive, Affective, and Behavioral Neuroscience, 5*(2), 144-155.

Tresch, M. C., Sinnamon, H. M., & Seamon, J. G. (1993). Double dissociation of spatial and object visual memory: Evidence from selective interference in intact human subjects. *Neuropsychologia, 31*, 211–219.

Umemoto, A., Drew, T., Ester, E. F., & Awh, E. (2010*).* A Bilateral Advantage for Storage in Visual Working Memory. *Cognition, 117,* 69-79.

Ungerleider, L. G., Courtney, S. M., & Haxby, J. V. (1998). A neural system for human visual working memory. *Proceedings of the National Academy of Sciences, U.S.A., 95,* 883–890.

Ungerleider, L. G. & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

Ventre-Dominey, J., Bailly, A., Lavenne, F., Lebars, D., Mollion, H., Costes, N., & Dominey, P. F. (2005). Double dissociation in neural correlates of visual working memory: a PET study*. Cognitive Brain Research, 25(3)*, 747-59.

Vogel, E. K. & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428*, 748-751.

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature, 438*, 500-503.

Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions, and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 92-114.

Weissman, D. H. & Banich, M. T. (2000). Cooperation between the cerebral hemispheres underlies the performance of complex but not simple tasks. *Neuropsychology, 14,* 41-59.

Weissman, D. H., Banich, M. T., & Puente, E. I. (2000). An unbalanced distribution of inputs across the hemispheres facilitates interhemispheric interaction. *Journal of International Neuropsychological Society, 6(3),* 313-321.

Wheeler, M. E. & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General*, *131*, 48-64.

Woodman, G. F. & Luck, S. J. (2004). Visual search is slowed when visuospatial working memory is occupied. *Psychonomic Bulletin & Review*, *11*, 269-274.

Woodman, G. F., Vogel, E. K., & Luck, S. J. (2001). Visual search remains efficient when visual working memory is full. *Psychological Science*, *12*, 219-224.

Xu, Y. (2002a). Limitations in object-based feature encoding in visual short-term memory. *Journal of Experimental Psychology: Human Perception and Performance, 28,* 458–468.

Xu, Y. (2002b). Integrating color and shape in visual short-term memory for objects with parts. *Perception & Psychophysics, 64*, 1260–1280.

Xu, Y. (2009). Distinctive neural mechanisms supporting visual object individuation and identification. *Journal of Cognitive Neuroscience, 21*, 511–518.

Xu, Y. & Chun, M.M. (2006). Dissociable neural mechanism supporting visual short-term memory for objects. *Nature, 440*, 91–95.

Xu, Y. & Nakayama, K. (2007). Visual short-term memory benefit for objects on different 3D surfaces. *Journal of Experimental Psychology: General, 136,* 653-662.

Zhang, H., Xuan, Y., Fu, X., & Pylyshyn, Z. W. (2010). Do objects in working memory compete with objects in perception? *Visual Cognition*, *18*(4), 617-640.

Zhang, W. & Feng, L. (1999). Interhemispheric interaction affected by identification of Chinese characters. *Brain and Cognition, 39,* 93–99.

Zhang, W. & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature, 452*, 233–235.