Visual working memory capacity is limited by two systems that change across lifespan

Anka Slana Ozimić, Grega Repovš

ABSTRACT

To better understand the sources of visual working memory limitations we explore the possibility that its capacity is limited by two systems: a representational system that enables formation of independent representations of visual objects, and an active maintenance system that enables sustained activation of the established representations in the absence of external stimuli. A total of 392 participants took part in four experiments in which they were asked to maintain orientation of items presented to the left, right or both visual hemifields. In all four experiments participants were able to maintain more items when they were distributed across both versus one visual hemifield, consistent with the proposal that bilateral display enables utilization of representational capacities of both hemispheres. Bilateral capacity, however, did not reach the combined representational potential of both hemispheres, indicating that the capacity is further limited by a second, unitary active maintenance system. Our study further suggests that both systems' capacities change throughout the lifespan very similarly. They both increase through development, reach a peak at the same age and decrease in healthy aging. This indicates that systems beyond executive processes, which receive most attention in the literature, are contributing to the decline in working memory in healthy aging.

Introduction

Working memory, the ability to maintain and actively manipulate a set of information needed to carry out current tasks, is one of the basic cognitive abilities (Baddeley, 1996a). It is used in everyday activities such as planning, reasoning, problem solving, reading and learning, and so forms the basis for goal-directed behaviour (Baddeley, 1996b). Working memory capacity changes throughout the lifespan and declines in healthy aging (Braver & West, 2007; Park & Festini, 2017). It correlates strongly with general intelligence (Cowan, 2005), and is among the first abilities affected in various diseases and injuries of the brain, from schizophrenia (Goldman-Rakic, 1994) to Parkinson’s disease (Bublak, Müller, Grön, Reuter, & von Cramon, 2002). Due to its central role in cognition, investigation of the core components and mechanisms of working memory is crucial for understanding of human cognition in both health and disease.

Working memory comprises a number of subsystems. Whereas the focus of working memory research was initially on verbal working memory, it has recently shifted to the study of visual and spatial working memory (Repovš & Baddeley, 2006). An important effort of this research is to understand the reasons for the highly limited capacity to maintain visual representations, which spans from three to five meaningful items in young adults, varies significantly across individuals (Cowan, 2010) and changes as a function of age (for review see Sander, Lindenberger, & Werkle-Bergner, 2012). Intense debates have arisen about the sources of the limitations, such as whether capacity is limited by a number of discrete representations or by an infinitely divisible resource (e.g. Luck & Vogel, 2013; Ma, Husain, & Bays, 2014), and whether the limitations reside in modality-specific working memory stores or general attentional processes (Cowan, 2010).

In this study we explore the possibility that visual working memory capacity is limited at two levels. First by the ability to form independent visual representations, and second by the ability to actively maintain them in the absence of external stimuli. Furthermore, we investigate how these two abilities change throughout the lifespan. We specifically focus on two questions relevant to the extant literature. First, whether the capacities of the two systems follow the same (e.g. Brockmole & Logie, 2013) or different (e.g. Hartshorne & Germine, 2015; Johnson, Logie, & Brockmole, 2010) development curves. Second, whether the capacity to actively maintain representations might show a more pronounced decline in healthy aging, which due to its closer relation to executive processes would be predicted by most of the literature.
A number of working memory models contributing to the understanding of the limitations of working memory capacity have been proposed. One of the most influential of these is Baddeley and Hitch (1974) multicomponent model of working memory. The model with its updates (Baddeley, 2000, 2012; Repovš & Baddeley, 2006) still form the main theoretical framework for the study of working memory within cognitive psychology. One of the essential contributions of the model is the division of working memory into four core components. Specifically, the central executive is regarded as a system of limited attentional capacity, which controls the entire system and focuses on and manipulates the relevant information in other subcomponents (Baddeley, 2012). The phonological loop, visuospatial sketchpad, and episodic buffer are assumed to be limited capacity subsystems responsible for storage and maintenance of verbal, visuospatial, and integrated information, respectively. Each component is assumed to consist of a passive store of limited capacity (e.g. phonological store, visual cache) and an active rehearsal process (e.g. articulatory control process, the inner scribe) (Logie, 2011; Logie & Van Der Meulen, 2009)—independent of the central executive (Bruyer & Scailquin, 1998; Klauer & Zhao, 2004)—that reactivates and helps maintain the degrading memory traces.

The multicomponent model considers working memory as a system separate though tightly integrated with long-term memory (Baddeley, 2012). In contrast, the so called “state-based” models (D’Esposito & Postle, 2015) assume that allocation of attention to internal representations either stored in long-term memory (e.g. Cowan, 1995; Oberauer, 2002, 2009) or established by the sensory-motor systems (Magnussen & Greenlee, 1999; Magnussen, 2000; Zakas, Bisley, & Pasternak, 2001) underlie the short-term maintenance of information in working memory. They further assume that the focus of attention, crucial for selection of mental representations to be held in working memory, can support only a limited number of activated representations. These models are consistent with recent neurophysiological findings on the roles of prefrontal and posterior areas of the cerebral cortex for the maintenance of information in visual-spatial working memory (Riggall & Postle, 2012). Specifically, studies indicate that posterior regions of the occipital and parietal cortex support the formation and/or temporary storage of visuo-spatial representations (Bettencourt & Xu, 2016), whereas prefrontal regions control the allocation of sustained attention to maintain relevant information (Erikkson, Vogel, Lansner, Bergström, & Nyberg, 2015).

Despite some key differences, both the multicomponent model of working memory as well as state-based models assume that two systems are involved in information maintenance. One enables the formation and storage of information representations, whereas the other its active maintenance or refreshing. The multicomponent model assumes (Baddeley, 2012; Logie, 2011) that representations are formed and maintained in component specific stores (e.g. phonological store, visual cache, episodic buffer) and that their active maintenance is enabled through the related rehearsal processes (e.g. subvocal rehearsal, the inner scribe). According to state-based models (D’Esposito & Postle, 2015) representations are established within either sensory-motor or long-term memory systems while the central executive supports their active maintenance in the focus of attention. Whereas both models acknowledge the relevance of the two systems, they differ in the specifics related to the source of working memory limited capacity.

In the multicomponent model of working memory, limited capacity is primarily explained “as an emergent property of the coordinated operation of the multiple components and may vary depending on which combination of components is deployed” (Logie, 2011, p. 242). Specifically, for the phonological loop, assuming trace decay, the capacity is “determined jointly by the durability of the memory trace and the time required to refresh the trace by subvocal rehearsal” (Baddeley, 2000, p. 419, Box 2). Whereas the phonological store itself is assumed to be of limited capacity (Baddeley, 2012), the process of refreshing itself does not seem to be encumbered by any limitations in the number of items it can (sub)vocalize, as long as they are still available in the store.

Analogous to the phonological loop, Logie (2011) proposes that the static content of the visual cache is limited by the visual complexity of the representation, which decays in about two seconds, if the constituting visually based codes are not mentally rehearsed by the inner scribe, which, however, is itself of a limited capacity. Based on multiple lines of evidence (for a review see Logie & Van Der Meulen, 2009) the dynamic content of the visuo-spatial sketchpad is proposed to further rely on the limited central executive resources.

The case of the episodic buffer is less clear, though. As explained by Baddeley (2012), the episodic buffer is believed to be—contrary to the initial assumptions—a passive system of limited capacity of three to four chunks for which active engagement of the central executive is only required when maintaining the binding against distraction. As Baddeley (2012) acknowledges, both the specific source of limitation—number of chunks or their similarity—as well as the process of rehearsal and maintenance of integrated information—currently speculated to rely on attentionally based refreshing—are, however, uncertain, as are their possible limitations.

State-based models (Cowan, 2005), on the other hand, assume that limitations in working memory primarily—if not exclusively—arise from the limited capacity of the focus of attention. Namely, the central executive can support active maintenance of the focus of attention for only a limited number of representations established in the essentially capacity-free sensory-motor or long-term memory systems, in which the activation of the relevant representations (i.e. activated memory) “is limited only by interference effects and possibly the passage of time” (Cowan, 2005, p. 42).

In this study, we directly explore the possibility that both systems (herein referred to as the representational system and active maintenance system) are of limited capacity and—resonating with Logie (2011)—that the final working memory capacity is determined by their interaction. This proposal echoes a recent proposal for a two-component framework by Sander et al. (2012) who, based on a review of lifespan differences in working memory and age-differential trajectories of posterior and frontal brain regions, conclude that multiple processes jointly limit visual working memory performance. The aim of this study is to explicitly test the proposed hypothesis that visual working memory capacity is jointly limited by capacities of two systems supporting working memory and to explore how these two systems interact and limit working memory capacity throughout development and healthy aging.

Active maintenance and representational potential: two limits of visual working memory capacity

As outlined above, we propose a conceptual model which assumes that two systems are engaged for information to be maintained in visual working memory. First, we propose the existence of a representational system that enables establishing independent representations of visual features and their bindings (e.g. colours, orientations, etc.)—analogous to the visual cache (Logie, 2011) and episodic buffer in the multiple component model (Baddeley, 2012) and sensory-motor or long term memory representational systems in state-based models (D’Esposito & Postle, 2015). Second, we propose the existence of an active maintenance system that enables ongoing activation of the representations established in the representational system in the absence of the external stimuli, and protects them from possible distractors—analogous to refreshing processes (e.g. visual scribe) and in some cases engagement of the central executive in the multiple component model (Baddeley, 2012; Logie, 2011), and the central executive directing attention to establish the focus of attention in state-based models (Cowan, 2005; D’Esposito & Postle, 2015).

Further, we propose that both systems present an independent
source of visual working memory capacity limitation. Specifically, we propose first that the representational system is able to establish only a limited number of independent representations at a given time, which sets the basic representational potential, the “upper limit”, for the capacity of visual working memory. As outlined in the previous section, in the multicomponent model of working memory (Baddeley, 2012) these limitations are proposed to be inherent to individual stores and present even in cases where the engagement of the central executive is not required.

Second, we propose that the active maintenance system itself possesses only limited resources available to focus on and actively maintain the established representations in the absence of external stimuli. This further limits visual working memory capacity, possibly preventing it from reaching its full representational potential. The evidence for the limitation of the active maintenance system is reviewed in detail in descriptions of state-based models (e.g. Christophel, Hebart, & Haynes, 2012), classical activation studies of visual working memory (e.g. Dolcos, Miller, Kragel, Jha, & McCarthy, 2007) show persistent dorsolateral prefrontal activity in the absence of distractors, while the level of delay related activation predicts task performance (e.g. Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002).

The key challenge in testing the proposed model of dual limits to working memory capacity is obtaining separate estimates of the capacities of the representational system and active maintenance system. To achieve that, we took advantage of the contralateral organization of the visual system—specifically, the fact that in the early stages of visual perception the information presented to the left visual hemifield is processed in the visual areas of the right hemisphere, and vice versa (Bullier, 2003). When both hemispheres are involved in the processing of visual information, as when the items to be processed are spread across both versus a single visual hemifield, a superior ability of visual encoding models (IEM) and multivariate pattern analysis (MVPA) show that the specific content of visual working memory is represented in various brain systems linked to perception (e.g. Christophel, Hebart, & Haynes, 2012), classical activation studies of visual working memory (e.g. Dolcos, Miller, Kragel, Jha, & McCarthy, 2007) show persistent dorsolateral prefrontal activity in the absence of distractors, while the level of delay related activation predicts task performance (e.g. Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002).

The hypothetical results of a visual working memory task illustrated within the proposed model in which an individual is asked to remember items presented to the left (remember left), right (remember right) or across both (remember both) visual hemifields, taking into account that across studies the capacity of visual working memory is estimated between three to four items. A: In the first scenario, the estimated capacity is always four items irrespective of where they were presented. The possible conclusions in this case are first, that active maintenance capacity is either equal or lower than the unilateral representational capacity, second, that the representational system is of an unlimited capacity, or third (not illustrated) that the representational system is not lateralized. B: In the second scenario the estimated bilateral capacity (four items) is equal to the sum of left and right unilateral capacities (two items each). The possible conclusions in this case are that the active maintenance system either has a capacity equal or higher than the limited representational potential across both hemispheres, or is of an unlimited capacity. C: In the third scenario the estimated bilateral capacity (four items) is higher than the unilateral capacity (three items), but lower than the bilateral representational potential, estimated as the sum of unilateral capacities (six items). In this case, the most parsimonious conclusion is that both the active maintenance system and the representational system are of limited capacity. Please note, that “torn” edges signify an unknown capacity / representational potential, that can be equal to or higher than the one pictured, and rounded edges a limited capacity/representational potential of the respective systems. Lightly coloured boxes represent established representations of visual features that, however, cannot be actively maintained.
processing known as bilateral field advantage can be observed. Bilateral field advantage was shown in a number of visual processing tasks such as orientation (Chakravarthi & Cavanagh, 2009) and letter identification (Kraft et al., 2013), multiple object tracking (Alvarez & Cavanagh, 2005) and enumeration of small sets of items (Railo, 2014). These studies point to existence of separate resources for left and right hemifields (Chakravarthi & Cavanagh, 2009) and are in line with suggestions that parallel processing is more efficient across hemifields versus within a single hemifield (Kraft et al., 2013).

Though both hemispheres are involved in the processing of higher-order visual information (Alvarez & Cavanagh, 2005) by exchanging information via the corpus callosum (Delvenne, 2012) regardless of the hemifield to which the information was presented, findings of several studies (e.g. Delvenne, 2012; Umemoto, Drew, Ester, & Awh, 2010; Vogel & Machizawa, 2004) suggest that analogously to the organization of early visual processing, the representations maintained in working memory are at least to some extent stored in the hemisphere contralateral to the visual field in which the information to be remembered was shown. For instance, a series of EEG studies (e.g. Vogel & Machizawa, 2004, for a review see Luria, Balaban, Awh, & Vogel, 2016), have repeatedly shown an increase in electrical activity, known as contralateral delay activity (CDA), above the parietal-occipital cortex of the hemisphere contralateral to the visual hemifield in which the to-be-remembered items are presented. Further, a number of studies have shown that participants are able to maintain more information in their visual working memory when the items to be remembered are distributed across both visual hemifields than if the same number of items are presented to one hemifield only. Such a bilateral field advantage effect has been demonstrated in tasks requiring the retention of spatial locations (Delvenne, 2005), orientations (Umemoto et al., 2010), and also colours (Holt & Delvenne, 2014). Moreover, Holt and Delvenne (2015) show that attentional pre-cues strongly influence both the transfer of items into visual short term memory—a feature of attentional selection—and their maintenance. It has recently been shown that bilateral display enhances both probability of storage of items as well as their precision (Zhang et al., 2017).

Taken together, these findings suggest that in early stages of visual processing the left and right hemispheres provide separate neuronal resources for visual representations of items presented to the right and left hemifield, respectively, and function—to at least some extent—as separate working memory stores, which when utilized in parallel enable bilateral field advantage. This enabled us to develop a more detailed model of visual working memory maintenance and propose specific hypotheses to test it (Fig. 1).

Specific proposals and hypotheses

Based on the review in the previous section, we have expanded our initial model with further specific assumptions. First, in line with a number of studies (e.g. Umemoto et al., 2010; Vogel & Machizawa, 2004, for a review see Delvenne, 2012), we assumed that items presented to a single hemifield are primarily encoded and represented in the contralateral hemisphere. Though each hemisphere can support only a limited number of independent representations, we further propose that the total number of possible visual representations across both hemispheres is determined by their joint capacity, which we refer to as bilateral (or full) representational potential of the representational system. Next, similar to state-based models (Cowan, 2005; D’Esposito & Postle, 2015), we assumed that the successful maintenance of representations is ensured by a single limited capacity active maintenance system that can independently maintain representations in any or both of the hemispheres. In our model, the final capacity is then determined by the number of independent representations established in the representational system, that the active maintenance system is able to actively maintain.

To test these assumptions, we designed a visual working memory task in which we asked the participants to encode and maintain visual items that were presented to left, right or both visual hemifields. Depending on the relationship between the single hemisphere’s representational capacity (unilateral representational capacity), bilateral representational potential, and active maintenance capacity, we identified three possible outcomes, visually illustrated in Fig. 1, each leading to a different conclusion about the validity of the proposed model.

First, if the number of items successfully recalled when they are presented to the left, right or both hemifields is the same, this can only be explained by two possibilities. Either—contrary to previously presented evidence—the representational system is not hemisphere specific but unified, or there is another system limiting the total number of sustained items at or below the capacity of unilateral representational systems. Within our proposed model we would conclude that it is the ability for active maintenance that is equal to or lower than the representational capacity of a single hemisphere (Fig. 1A). In such a case we could not differentiate between two alternative possibilities regarding the limits of the representational system. One possibility is that the representational system is of limited capacity, however the limit of each unilateral representational system exceeds the limits of the active maintenance system. Another possibility is that the representational system itself is unlimited.

Second, if the number of items successfully recalled, when they are presented across both visual hemifields, is equal to the sum of items successfully recalled when presented to the left and right visual hemifields alone, this could only be explained by either the absence of an additional limiting system or by the limit of such a system being equal to or exceeding the limits of the representational system. Specifically, based on our model (Fig. 1B), we would conclude that the capacity of active maintenance is equal to or exceeds the bilateral representational potential or is itself of unlimited capacity.

Third, if the number of items successfully recalled, when they are presented across both visual hemifields, is larger than when the items are presented to either hemifield alone, but smaller than their joint representational potential, this suggests that visual working memory is limited at two levels. If a system was limited at the representational level only, then a full bilateral capacity should be reached, when the items are presented across both hemifields. If a system was limited at the maintenance level only, then the same limit should be observed in unilateral and bilateral presentation. Therefore, based on our model (Fig. 1C), we would conclude that the capacity of active maintenance system exceeds the representational capacity of individual hemispheres but is lower than their joint bilateral representational capacity. Again, such a situation would present strong evidence that visual working memory is limited at two levels. By extension this would provide support in favour of the proposed model itself, specifically, for the claim that visual working memory capacity is limited both by the limited ability to form independent visual representations, as well as the limited ability for their active maintenance.

In the case of the third outcome, which we argue would suggest two limits of visual working memory capacity, the sum of the unilateral capacities indicates the potential maximum of items a person can represent and so can be used as a measure of the representational system’s capacity. The bilateral capacity on the other hand directly reflects the limits of the active maintenance system, and so can be taken as the measure of the active maintenance system’s capacity.

Age-related changes of working memory capacity

Observing working memory capacity throughout the lifespan provides important information both about healthy aging as well as the component structure and processes of working memory. In addition to testing the proposition that visual working memory capacity is jointly limited by the representational and active maintenance systems, the aim of our study was also to explore how these two systems interact and
limit working memory capacity throughout development and healthy aging. Specifically, we were interested in to what extent changes in working memory capacity with age reflect changes in the ability of the representational system to form independent representations, and to what extent they reflect changes in the capacity for their active maintenance. The comparison of their developmental curves further enabled us to address open theoretical and empirical questions regarding the development of visual working memory capacity, as well as its decline in healthy aging.

A large study assessing cognitive abilities throughout the lifespan (Hartshorne & Germine, 2015) shows that different abilities, including performance on a number of working memory tasks, peak at different ages. Johnson et al. (2010), employing a range of tests tapping into different working memory modalities and processes, report that whereas a single common factor could be observed throughout the lifespan, it did not contribute consistently to test performance across age, indicating that specific abilities change with different trajectories leading to their differential use at different stages of development.

Alloway and Alloway (2013) employed a verbal and visual working memory task requiring maintenance and manipulation across a large sample of subjects aged five to 80. They discovered that a structural model with latent visual and verbal components explained the data better than models assuming a single working memory factor or separate maintenance and manipulation components. In contrast Swanson (2017), though observing steeper rise and decline in visuo-spatial than verbal working memory performance, reported that confirmatory factor analysis best supported a domain general factor across children and adult groups.

Brockmole and Logie (2013) focused specifically on visual working memory in a large sample of eight- to 75-year-olds. They found that memory for individual (colour and shape) features and their binding follows the same developmental curve. The authors concluded that a decline in colour-shape binding is driven largely by a decline in the capacity for maintenance of individual features. As the percent of bound features in memory also changes throughout development, it is thought possible that maintenance of individual features and their binding in working memory are subserved by separable systems.

Reviewing a number of studies on aging as well as their own research, Sander et al. (2012) propose that changes in working memory throughout the lifespan should be understood as the result of an interplay between two components of working memory, low-level feature binding processes and top-down control. In our model, these could be mapped to our distinction between the representational system and active maintenance system, respectively. The authors (Sander et al., 2012) point out a lack of studies investigating both ends of the lifespan with the same paradigm, and suggest that the differentiation and specification of the two components, and interactions between them, presents an important research question.

Specific predictions related to lifespan changes in working memory capacity

The ability to separately estimate the capacities of the two systems afforded by our visual working memory span task provides a unique possibility to study how the interaction between the two systems changes throughout development and aging. Specifically, a decline in cognitive abilities in healthy aging has been mostly ascribed to reduced ability of executive processes (Braver & West, 2007). A recent study by Rhodes et al. (2019), for instance, finds that the cost of concurrent processing tasks on maintenance of items in working memory increases with age. In this case, with advanced aging, we would expect the visual working memory capacity to be primarily limited by the ability of active maintenance of visual representations, reflected in a reduction or even absence of bilateral advantage.

Sander et al. (2012) provide a more nuanced prediction of the change in the two systems capacities throughout the lifespan, expecting representational potential to be already close to maximum capacity early in development, and active maintenance capacity to have a more pronounced peak later in development, both decreasing significantly in older adults. This would predict an initial rise and a subsequent decline in the observed bilateral advantage.

A study by Souza (2016), investigating attentional and maintenance processes in young and older adults, finds that though baseline capacity to retain colours in visual working memory declined in older adults, their ability to use the attentional pre- and post-cues remained the same. Assuming that the decline in baseline capacity reflects a decline in the representational system and the retained ability to use attentional cues a stable active maintenance system, this would predict bilateral advantage to increase in aging, possibly to the point where it reaches full representational potential.

Overview of the present study

Using a lateralized working memory span task for orientations, we conducted four experiments. The aim of Experiment 1 was to test our basic assumption that working memory capacity is limited by two systems. The aim of the Experiment 2 was to additionally assess age-related changes in the two systems by including a larger sample of participants that spanned ages from 10 to 70. In Experiments 1 and 2 we used spatial pre-cues which were shown to be important in inducing bilateral advantage (Holt & Delvenne, 2015) by allowing participants to allocate their attention to target locations prior to their presentation. Spatial pre-cues, however, also provided participants with an opportunity to move their gaze toward targets, which could result in bilateral encoding of unilaterally presented stimuli, and invalidation of the key experimental manipulation. To address this concern, a subset of participants taking part in Experiment 1 was tested again in Experiment 3 in which no spatial pre-cues were presented. Our reasoning was that if subjects are not forewarned about the location of the targets, they are less likely to shift the gaze to their location. However, Experiment 3 could not entirely exclude the possibility that the participants moved their gaze to the target location once they were shown it. For that reason we conducted Experiment 4 in which we used an eye tracker to explicitly control for eye movements. This enabled us to more robustly address the initial question without the concern of undesired target stimuli fixations, as well as investigate the role of spatial pre-cue.

Experiment 1

The aim of Experiment 1 was to test our basic assumption that two systems—purportedly a representational and an active maintenance system—limit working memory capacity. The experiment involved a homogeneous group of participants in terms of age and education and included the use of spatial pre-cues to indicate the location of the to-be-presented target items.

Method

Participants

Sixty-two psychology students (55 females) aged between 19 and 22 ($M = 19.6, SD = 0.89$; years of education: $M = 13.2, SD = 0.55$) signed an informed consent to participate in a 15-minute experimental session in which they completed a visual working memory span task. All participants had normal or corrected to normal eyesight. None of the participants reported any neurological illnesses or conditions. All but two participants were right handed. The sample size was determined by the number of students in the Cognitive Psychology lab course that agreed to participate, with the expectation that it would match or exceed the sample size in similar studies (e.g. Delvenne, 2005; Holt & Delvenne, 2014, 2015; Kraft et al., 2013; Zhang et al., 2017). The participants did not receive any compensation for participation in the study. The study was approved by the Ethical Committee of the Faculty of Arts, University of Ljubljana.
They confirmed and were able to change them until they were satisfied with their reconstruction with a mouse-click on the fixation point. Feedback was given by changing the colour of the fixation point briefly (500 ms) to either green (for a correct response) or red (for an incorrect response), before turning to light grey, indicating the rest period. Both the accuracy and reaction times of the responses were recorded, though reaction times were not analysed.

Two main factors were manipulated in the task: target location, which corresponded to the side of the screen on which the target stimuli were shown (left, right, up, down), and load, corresponding to the number of targets presented in the trial. The targets were always presented in a contiguous group around the virtual circle (see Fig. 2). When the load was even the targets were presented in equal numbers on both sides of the 12, 3, 6, and 9 o’clock positions, for top, right, down and left presentations, respectively. For odd loads, the odd target was sometimes presented immediately clockwise, other times immediately counter-clockwise from the main group, with the exact position changing randomly from trial to trial.

For each of the target location conditions (left, right, up, down) visual working memory span was estimated separately using the following procedure. For each target location the procedure started with an initial load of one item. If the first trial at a given load was successful, the load was increased by one. If the first trial at a given load was unsuccessful, the participant was given up to four additional chances at that load. If three attempts at a given load were successful, the load was increased by one. If none of the five attempts at a given load were successful, the load was decreased by one. Once five attempts were made at the highest load in which the subject made at least one successful attempt, the estimation procedure for that target set location ended and the span was estimated using the formula:

\[ K = (L_{\text{max}} - 1) + \frac{S_{\text{max}}}{N_{\text{max}}} \]  

(1)

where \( L_{\text{max}} \) is the maximum load achieved, \( S_{\text{max}} \) is the number of successful trials at maximum load (at least 1) and \( N_{\text{max}} \) is the number of attempts at the highest maximum load (always five). The location of the target set probed changed randomly from trial to trial until spans were estimated for all four target set locations.

Procedure

After signing the consent form, the participants were told how to perform the task. The experimenter presented them with examples of the visual working memory span task until they reported they were confident they knew how to perform the task. The participants then completed the test part of the task in which the visual working memory span was estimated, as described above. By observing the participant throughout the task performance, the experimenter ensured that the participants were seated so that the screen was centred with respect to their face and body orientation.
Results

Bilateral capacity exceeds unilateral capacity

First, we assessed whether there is an advantage in working memory performance when stimuli are presented bilaterally in comparison to unilateral presentation (Fig. 4A). The results of the one-tailed paired t-test revealed significantly higher K for bilateral versus unilateral target location conditions, *t*(61) = 8.92, *p* ≤ .001, *d* = 1.13. Note that each individual’s lower unilateral capacity KM\textsubscript{IN} = min(KL, KR) was used in the test. The reason for using KM\textsubscript{IN} is that it is both sufficient as well as the most sensitive test of the hypothesis that active maintenance capacity (estimated by K\textsubscript{B}) exceeds the capacity of any individual unilateral representational system (estimated by KL and KR). The test is sufficient as we only need to show that the estimated active maintenance capacity exceeds the capacity of at least one of the unilateral representational system to conclude that capacity is already limited at the level of the representational system. It is also the most sensitive, as in the case of a difference between capacities of the left and right unilateral representational systems, when the capacity of the active maintenance system might exceed the capacity of the lower performing but not the higher performing unilateral representational system, which would reduce the otherwise present effect of interest.

Though, as argued above, KM\textsubscript{IN} is the most relevant measure of unilateral representational system capacity for the purpose of addressing the current research question, we additionally checked whether the bilateral capacity is higher than unilateral capacity when compared to the average unilateral capacity K\textsubscript{AVG} = mean(KL, KR) or the capacity of the better performing hemisphere K\textsubscript{MAX} = max(KL, KR). The one-tailed paired t-test confirmed that bilateral capacity is also higher than both average unilateral capacity, *t*(61) = 6.49, *p* ≤ .001, *d* = 0.82, as well as each individual’s maximum unilateral capacity, *t*(61) = 2.61, *p* = .006, *d* = 0.33.

Bilateral capacity does not reach full representational potential

Further, we tested whether the working memory capacity for the bilateral target location condition reaches the participants’ unilateral

All analyses were performed in R (R Core Team, 2014), using built-in functions \texttt{t.test, lm, shapiro.test, ks.test} and \texttt{wilcox.test} for t-test, linear regression, Shapiro-Wilk test, Kolmogorov-Smirnov test and Wilcoxon Rank-Sum, respectively. The \texttt{ezANOVA} function of the \texttt{ez} library (Lawrence, 2013) was used for ANOVA analyses, \texttt{cohensD} function from \texttt{lm} library (Navarro, 2015) for computing Cohen’s \texttt{d} effect size and \texttt{lme} function of the \texttt{lme4} library for generalized linear mixed-effects models (Bates, Mächler, Bolker, & Walker, 2015). Data were visualized using \texttt{ggplot2} library (Wickham, 2009).
representational potential (Fig. 5A, left). We used a one-tailed one-sample t-test to compared the bilateral capacity index against 1, corresponding to full representational potential (RP). As in theory bilateral capacity index (CIB) is limited to 1, the use of a t-test in this situation would not be appropriate when CIB would be close to 1, as its distribution could be highly asymmetrical. The results though showed that CIB is normally distributed, $W = 0.98, p = 0.355$. The analysis revealed that bilateral capacity index is significantly lower than 1, $t (61) = -52.4, p \leq 0.001, d = -6.66$, confirming that, across participants, bilateral capacity does not reach the full bilateral representational potential.

**Unilateral capacity differs between hemispheres**

To test whether there were systematic differences between the capacities estimated for left and right visual hemifields (Fig. 4B), we computed a two-tailed paired t-test between $K_L$ and $K_R$. The results showed a somewhat higher capacity when items were presented to the left visual field, $t(61) = 2.02, p = .048, d = 0.26$. Similarly, we checked for significant differences in $K$ when presenting stimuli above ($K_U$) versus below ($K_D$) the fixation point (Fig. 4B). A two-tailed paired t-test did not reveal significant differences between $K_U$ and $K_D$, $t (61) = 0.524, p = .602, d = 0.07$. Further, we investigated whether the difference in the measured capacity depending on the position of the presented items differs between unilateral and bilateral presentation. A two-tailed paired t-test comparing the absolute difference between $K_L$ and $K_R$ with the absolute difference between $K_U$ and $K_D$ did not reveal significant differences, $t(61) = -1.44, p = .155, d = 0.18$.

It is possible that hemispheric differences in estimated unilateral capacity differ across individuals not just in magnitude, but also in primacy. To visualize the imbalance between the unilateral capacities of the two hemispheres, we plotted a distribution of absolute differences between them. More specifically, to take into account individual differences in overall working memory capacity we computed the absolute difference between $C_{IL}$ and $C_{IR}$. Additionally, to test whether the differences between “dominant” and “non-dominant” hemispheres are significant across participants, we created a comparison normal distribution and tested whether the two distributions differed significantly.

Specifically, we estimated a standard deviation of a complete distribution of differences by combining the original set of absolute differences in unilateral CI with a mirror set (all values were multiplied by −1) and computing the standard deviation of the new set. We then created a normally distributed random sample of 10,000 values with a mean of 0 and the previously estimated standard deviation, and converted the set to absolute values. This now served as a null distribution, which we would expect to get if the differences between the unilateral CIs were normally distributed. We then compared the two distributions using a Kolmogorov-Smirnov test. Significant differences between the two distributions would indicate that the differences between the unilateral CIs are not random, and that across individuals in the sample the unilateral capacity of hemispheres differs significantly. The results shown in Fig. 6 confirm the significant difference from an expected trimmed normal distribution with a mean of 0.

**Bilateral capacity index varies across individuals**

Lastly, a comparison of the bilateral capacity index across participants revealed marked differences in their ability to use both hemispheres’ full representational potential (Fig. 5A, right). We further explored this variability. Specifically, we hypothesized that individuals with lower unilateral representational capacity are able to utilize their full representational capacity in the case of the bilateral presentation of targets to a larger extent in comparison to individuals with a higher unilateral representational capacity. In the latter case, due to the limits of the active maintenance system, we would predict that the individuals with a high unilateral representational capacity have fewer resources free to take advantage of the bilateral encoding of stimuli.
To test this possibility, we computed a linear regression model, predicting the bilateral capacity index ($C_{IB}$) from representational potential ($RP$) (Fig. 7). Based on Formula (2), if bilateral capacity ($K_B$) is not dependent on the capacity of the active maintenance system, but rather reflects a fixed proportion of the full representational potential ($RP$), then the $C_{IB} = K_B/(K_L + K_R)$ should stay constant and the $\beta$ in the linear regression should be 0. Alternatively, if the extent of bilateral advantage indeed depends on the magnitude of the representational potential, then we should observe the $\beta$ to be significantly lower than 0.

The results confirm a slight but significant decrease in the bilateral capacity index with an increase in representational potential, $t(61) = -3.13, p = .003, \beta = -0.03, R^2_{adj} = 0.13$, reflecting that participants with a higher representational potential have more difficulties in utilizing both of their hemispheres' capacities in the case of the bilateral presentation of stimuli, leading to a smaller bilateral advantage.

Discussion

The goal of this experiment was to investigate whether working memory capacity is limited at two levels. Specifically, as suggested by our model, by the ability to form independent visual representations as well as the ability for their active maintenance. Previous studies (for a review see Luria et al., 2016) indicate that maintenance of visual information follows the hemispheric organization of the visual system, and is supported by two independent representational systems. By estimating the capacity when either or both of the representational systems were engaged, we argued that the results in a case when the observed bilateral capacity is higher than the individual unilateral capacity but lower than the joint bilateral representational potential can only be explained by visual working memory being limited at two levels. Additionally, such a result would indicate that it is possible to obtain separate estimates of the representational potential, and the capacity for active maintenance.

As expected, the results revealed higher estimates of working memory capacity, when stimuli were presented across both versus a single hemifield, by utilizing the representational potential of both representational systems. Though each individual’s lower unilateral capacity, $K_{MIN}$, was considered as the key measure for unilateral capacity, we additionally showed that bilateral capacity also exceeds both the average unilateral capacity $K_{AVG}$ as well as the capacity of the better performing hemisphere $K_{MAX}$. This provides robust evidence that in the case of visual working memory its total capacity—in our model reflecting the capacity of the active maintenance system—is higher than the capacity of any of the individual unilateral representational systems.

Next, we showed that bilateral capacity did not reach the full representational potential, defined as the sum of unilateral representational capacities. Among the three theoretical possibilities, namely, that the capacity is limited by the representational system, the active maintenance system, or both, the obtained results strongly indicate the latter. Specifically, the results supported the proposition that the capacity for active maintenance exceeds the capacity of each hemispheric representational system, but is lower than their joint representational potential.

For comparability with previous research on bilateral field
advantage (e.g. Holt & Delvenne, 2015), we additionally tested for possible systematic differences between capacity estimates when stimuli are presented to the left versus right visual hemifields as well as above versus below the fixation points. The results did not reveal significant differences between the capacities for upper and lower visual hemifields, justifying our decision to average the two as the relevant measure of bilateral capacity. The results, however, did show significant differences between the capacity for the left and right visual hemifields in favour of the left. The significant difference between the capacity of the two hemifields was additionally confirmed by an analysis of the distribution of differences in unilateral capacity indices with no assumption about the dominance of a specific hemifield, which can potentially vary across participants.

The observed hemispheric dominance provides additional evidence that the visual working memory capacity is limited at the level of the representational system. Specifically, if the capacity of the visual working memory was limited only by the active maintenance system, no differences in capacity should be observed when presenting items to the left versus right visual fields. The observed results therefore indicate that left and right hemispheres have—at least to some extent—indeed independent representational systems with limited capacity.

Further exploration of the results revealed noticeable differences in the participants’ bilateral capacity indices. In other words, the relationship between the participants’ bilateral capacity and representational potential was not constant across participants, suggesting that participants differ in their ability to use their full representational potential. The observed negative relationship between the bilateral capacity index and the representational potential supported our assumption that individuals with lower unilateral representational capacity have more free resources of the active maintenance system left to take advantage of bilateral representation, leading to higher bilateral advantage.

**Experiment 2**

The results of Experiment 1 suggested that the capacity of visual working memory is limited by both the ability to form independent visual representations as well as the ability for their active maintenance. These findings, together with the observation of high inter-individual variability in terms of bilateral advantage, open new questions and possibilities for the study of working memory in aging and disease.

The aim of the second experiment was to replicate the results of Experiment 1 in a larger, heterogeneous sample of participants, and to explore changes in working memory capacity throughout development and healthy aging. Specifically, we focused on the question of to what extent previously observed changes in working memory capacity with age reflect changes in the ability of the representational system to form independent representations, and to what changes in the capacity for their active maintenance. Additionally we explored how the developmental curves match with existing empirical findings and theoretical possibilities for the study of working memory in aging and disease.

To address these questions, we first assumed that a difference in representational capacity should be reflected in a significant relationship between unilateral working memory capacity and age. Importantly, this assumption depends on the capacity of the active maintenance system (reflected in the bilateral working memory capacity, $K_{AB}$) to exceed the unilateral representational potential. If this assumption is not met, the observed working memory capacity would only reflect the capacity of the active maintenance system (see Fig. S1B) and underestimate representational capacity. Given the observed differences in the capacities of the left and right unilateral representational systems, this assumption is less likely to be violated in the case of the lower performing hemisphere. For this reason, we have specifically focused on the relationship of age with $K_{MIN}$.

Second, we have assumed that a difference in the capacity of the active maintenance system should be reflected in the bilateral capacity index. Specifically, if there is no difference in representational potential across age then the bilateral capacity index should be reduced when the capacity of the active maintenance system is reduced (see Fig. S1B). The situation is more complex in the case of an observed reduced unilateral representational capacity with age. In such a case, if the capacity of the active maintenance system is constant then the bilateral capacity index should increase with age (see Fig. S1A). Alternatively, a decrease in the bilateral capacity index would indicate a disproportionally larger decrease in the active maintenance capacity compared to the unilateral representational potential.

To validate the described hypotheses and better understand the relationships between possible changes in unilateral representational and active maintenance capacities, as well as the resulting estimates of working memory capacity and bilateral advantage, we performed a simulation testing a number of key scenarios (see Supplemental Information and Fig. S1), as well as exploring the space of possible parameters (Fig. 8). The results validate the hypotheses presented above.

**Method**

**Participants**

Two hundred and nineteen participants (130 females) aged between 10 and 70 ($M = 33.1, SD = 19.1$; years of education: $M = 12.5$, $SD = 4.0$) participated in Experiment 2. All participants had normal or corrected to normal eyesight. None of the participants reported any neurological illnesses or conditions. Based on the visual inspection of results, none of the participants was identified as an outlier in their age group on their summary QFC (Cognitive Failures Questionnaire) or measures of verbal WM span, Stroop colour-word tasks, Trail Making Task, Verbal Fluency, Visual Search or Tower of London task. All but 13 participants were right handed. Tests were administered by students of psychology as part of their lab course. Before the start of data collection all the students conducted all the tests themselves. Additionally, the students received both detailed written instructions as well as hands-on training in the use of the instruments, the study protocol, and the importance and practice of obtaining informed consent. We emphasized that the prospective participants, even if they were interested in performing the task, were in no way obliged to sign an informed consent form, and that their data would not be used in that case. Each student

![Fig. 8. Estimated linear rate of change in bilateral capacity index ($C_{BA}$) for a parameter space of simulated decreases in active maintenance ($C_{MA}$) and unilateral representational ($C_{AR}$) systems’ capacities. Notice that bilateral capacity index increases when both unilateral and active maintenance systems decrease at the same rate. A stable rate of decreases in bilateral capacity index is only observed when active maintenance capacity decreases at a faster rate than the capacity of the unilateral representational system.](image-url)
was tasked to recruit and test four participants from four distinct age groups. In this manner the data collection protocol was designed to recruit a heterogeneous and large sample of participants of different ages. The final sample size reflects the number of participants that passed the exclusion criteria, for which all the relevant data was properly collected, and the participants gave their signed informed consent. The study was approved by the Ethical Committee of the Faculty of Arts, University of Ljubljana.

Apparatus, materials, task and procedure were the same as in Experiment 1, with the exception that all the participants were tested outside of the laboratory, mostly in their home environments.

Results

Bilateral capacity exceeds unilateral capacity and does not reach full representational potential

To replicate the results from Experiment 1, we first checked for an advantage in working memory capacity when stimuli are presented bilaterally versus unilaterally (Fig. 4A). A one-tailed paired t-test revealed significantly higher capacity for bilateral (K\text{B}) versus unilateral (K\text{MIN}) target set location conditions, t(218) = 14.6, p ≤ .001, d = 0.989.

Next, we tested whether the working memory capacity for bilateral presentation reaches the participants’ bilateral representational potential (Fig. 5B). As the CIB scores did not significantly deviate from the normal distribution, W = 0.99, p = .107, we used a one-tailed one-sample t-test, which revealed that bilateral capacity index is significantly lower than 1, t(218) = -107.6, p ≤ .001, d = -7.27, confirming that, across participants, bilateral capacity does not reach the full bilateral representational potential.

Lastly, as the relationship between the participants’ bilateral capacity and representational potential, i.e. the bilateral capacity index, was not constant across participants, we computed a linear regression model to test whether representational potential (RP) is negatively associated with bilateral capacity index (CIB), with an increase in the representational potential, t(217) = -3.05, p = .003, \( \beta = -0.02, R^2_{\text{adj}} = 0.04 \). Together, these results fully replicate those from Experiment 1.

Both unilateral and bilateral working memory capacity change across lifespan

We used linear regression to explore how the working memory capacity of both systems changes throughout development and healthy aging. Specifically, we built a linear regression model predicting the measured visual working memory capacity with the factors of age and target location (bilateral vs. unilateral), and subject as a random factor. Note that due to the reasons explained above we used K\text{MIN} as the working memory capacity estimate in the unilateral target presentation condition. Due to the expected and observed (Fig. 9A) nonlinear relationship of working memory capacity with age, we used a forward selection procedure to select the appropriate hierarchical regression model.

A fourth-degree polynomial regression model best fitted our data, \( \chi^2(5) = 230.0, p < .001, R^2_{\text{adj}} = 0.814, \beta_{\text{age}^4} = -3.36, \beta_{\text{age}^3} = -2.96, \beta_{\text{age}^2} = 1.35, \beta_{\text{age}} = -1.63 \), for the fourth-degree polynomial relationship with age, and \( \beta_{\text{bilateral presentation}} = 0.310 \) for target location. To test whether the capacities of the two systems evolve differently with age, we compared models with and without the age \( \times \) target location interaction. Though we cannot exclude the possibility of an interaction, this comparison did not provide clear evidence for one, \( \chi^2(4) = 9.36, p = 0.053, R^2_{\text{adj}} = 0.016 \). To test the effect of age, we compared models with and without the inclusion of age, and the results yielded a significant effect of age, \( \chi^2(4) = 80.0, p < .001, R^2_{\text{adj}} = 0.27 \). To test the difference between unilateral and bilateral target presentation, we compared models with and without the factor of target location, which yielded a significant effect of target location \( \chi^2(1) = 150.0, p < .001, R^2_{\text{adj}} = 0.53 \). Together the results reflect a rapid increase in visual working memory capacity through childhood and adolescence, a slow decrease through early and middle adulthood, and finally, a rapid decrease in late adulthood. Bilateral presentation of target stimuli resulted in significantly higher working memory capacity than unilateral presentation throughout the lifespan. The predicted peaks of unilateral and bilateral capacity, based on separate fourth-degree regression models, were 22.75 and 22 years, respectively.

Further, we also tested whether the bilateral capacity index (CIB) changes as a function of age. A forward selection procedure was used to build a hierarchical regression model. The linear regression model best fitted our data, F(1, 217) = 4.00, p = .047, R^2_{\text{adj}} = .02, revealing a slight but significant decrease in CIB across lifespan, \( \beta = -0.0005, t (217) = -2.0 \) (Fig. 9B).

As different memory capacities and related processes can be differentially affected during development, early adulthood and healthy aging (Johnson et al., 2010), we have—based on estimated peak performance at year 22 and an apparent inflection point at year 50—repeated the above analyses for three age groups: 10 to 22 (young), 23 to 50 (adult) and 51 to 70 (aging). Whereas in the young group memory capacity was best modelled using a second-degree polynomial, \( \chi^2(3) = 126.48, p < .001, R^2_{\text{adj}} = 1.08, \beta_{\text{age}^2} = 2.18, \beta_{\text{age}} = -1.63 \), \( \beta_{\text{bilateral presentation}} = 0.379 \), for the adult, \( \chi^2(2) = 44.58, p < .001, R^2_{\text{adj}} = 0.517, \beta_{\text{age}} = -0.012, \beta_{\text{bilateral presentation}} = 0.262 \), and the aging, \( \chi^2(2) = 33.07, p < .001, R^2_{\text{adj}} = 0.479, \beta_{\text{age}} = -0.029, \beta_{\text{bilateral presentation}} = 0.232 \) the groups’ linear models sufficed. In all three groups age—young: \( \chi^2(2) = 24.67, p < .001, R^2_{\text{adj}} = 0.194 \); adult: \( \chi^2(1) = 7.54, p = .006, R^2_{\text{adj}} = 0.434 \); aging: \( \chi^2(1) = 13.46, p < .001, R^2_{\text{adj}} = 0.169 \)—as well as target location—young: \( \chi^2(1) = 101.81, p < .001, R^2_{\text{adj}} = 0.920 \); adult: \( \chi^2(1) = 37.041, p < .001, R^2_{\text{adj}} = 0.434 \); aging: \( \chi^2(1) = 19.62, p < .001, R^2_{\text{adj}} = 0.282 \)—were significant predictors of the estimate of working memory capacity, whereas no age \( \times \) target location interaction was observed (all \( p > .20 \)).

We used the fourth-degree polynomial regression model, fitted separately for the estimated bilateral (K\text{B}) and unilateral working memory capacities (K\text{MIN}), to compute the predicted unilateral and bilateral capacities at three time points: their peaks, at 50 and at 70 years of age. Based on the estimated capacities, we computed their yearly decline in adulthood and healthy aging. As shown in Table 1, the yearly decline is more pronounced in aging, and relative declines for unilateral and bilateral capacities are comparable.

Separate linear regressions of age on bilateral capacity index (CIB) for the three age groups revealed no significant relationship for the young, F(1, 99) < 1, \( p = .440, \beta = 0.0013, R^2_{\text{adj}} = -.004 \), the adult, F(1, 67) < 1, \( p = .808, \beta = -0.0001, R^2_{\text{adj}} = -.014 \), or the aging, F(1, 47) < 1, \( p = .694, \beta = -0.0006, R^2_{\text{adj}} = -.018 \), groups. The relationship of bilateral capacity index (CIB) with age was effectively flat.

Discussion

The goal of this experiment was, first, to replicate the results of Experiment 1 in a larger heterogeneous sample of participants, and second, to explore changes in visual working memory capacity through the lifetime as a function of the changes in the two proposed systems. Experiment 2 fully replicated the findings of Experiment 1. The results showed higher bilateral versus unilateral working memory capacity, i.e. bilateral field advantage, suggesting a limited capacity of unilateral representational systems. Next, we showed that bilateral capacity did not reach the full representational potential, supporting the proposal that visual working memory capacity is limited by an additional, active maintenance system. Moreover, the results replicate initial finding of a significant relationship between bilateral capacity index and representational potential, suggesting that participants with lower representational capacity can more fully employ the capacities of both hemispheres in the case of bilateral presentation of the stimuli.
Next, we focused on the question of whether differences in working memory capacity across age reflect differences in capacity to form independent representations (assessed by unilateral capacity, \( K_{\text{MIN}} \)), differences in the capacity for active maintenance (reflected in bilateral capacity \( K_B \)), or both. The results showed a significant and similar relationship of both \( K_{\text{MIN}} \) and \( K_B \) with age, revealing that the representational system’s capacity as well as active maintenance system’s capacity change throughout the lifespan.

Whereas the age of peak performance closely matches that obtained by Brockmole and Logie (2013), in contrast to their data, showing a linear decline in maintenance of individual features and their binding, in our study we observe an intermediary plateau between the ages of 40 and 50 and differential rates of decline in adulthood and healthy aging for both unilateral and bilateral capacities. A possible explanation for the observed differences, and one that would require empirical testing to confirm, could be differences in the task requirements and related working memory processes engaged by the two tasks.

As emphasized by Johnson et al. (2010) the differences in decline in the capacity of different components and processes of working memory in later adulthood are of key interest. Our results indicate a significant decrease in both representational potential and active maintenance capacity in adulthood and healthy aging. Though we observed a small but significant decline in the bilateral capacity index (\( C_{\text{BI}} \)) across lifespan, the relationship was basically flat both in adulthood and healthy aging. Based on the lack of a significant interaction between unilateral and bilateral capacity, there is no evidence of a differential decline in the two systems. However, as the results of the simulation indicate (Fig. 8), a flat relationship between bilateral capacity index and age is more consistent with a steeper decline in active maintenance capacity than the unilateral representational potential. Additionally, due to the nature of the relationship, the lack of a significant negative relationship between age and bilateral capacity index could be due to a floor effect—also observed in the simulation (Fig. 8)—and the observed significant individual variation in bilateral advantage. Thus, the possibility of a steeper decline in active maintenance capacity cannot be ruled out, and should be further investigated using novel experimental designs or longitudinal studies.

Whereas our span task followed the design of a series of other experiments employing a change detection paradigm (for a review see Delvenne, 2012; Luria et al., 2016) we identified a potential issue in the study design that could affect the obtained results. Specifically, though the participants were asked to fixate their gaze at the fixation point in the centre of the screen throughout the trial, we had no means to control and enforce their compliance. If the participants failed to follow instructions and shifted their gaze to the side of the screen relevant for a particular trial, as indicated by a pre-cue, this could lead to bilateral encoding of stimuli even in nominally unilateral encoding conditions. Such a situation would result in overestimation of both hemispheres’ unilateral capacities, as well as full representational potential. It would consequently result in underestimation of the bilateral capacity index, as an indicator of bilateral encoding advantage.

To address this concern, we designed a third experiment in which we did not provide a spatial pre-cue before the presentation of the target items in order to minimize the possibility that the participants would direct their gaze toward the target items.

### Experiment 3

In Experiments 1 and 2, the location of the participants’ gaze at the time of the target presentation was not controlled. As the location of the target set was indicated using a location pre-cue, this could lead the participants to move their gaze away from the fixation point to the location of the to-be-presented target set. In such a case the items would be encoded bilaterally, which could inflate the estimates of capacity for the unilateral presentation (\( K_R, K_L \)) and representational potential, and lead to underestimation of the bilateral capacity index (\( C_{\text{BI}} \)).

To minimize the possibility of fixation on the target items, we repeated Experiment 1 without providing a spatial pre-cue before their presentation. Even though previous studies have shown that attentional pre-cues strongly influence bilateral advantage in change detection working memory tasks (Holt & Delvenne, 2015), to the best of our knowledge span tasks have never been used to test for the presence of bilateral advantage, and the role of a spatial pre-cue is not known in this context.
Method

Participants
The participants who took part in Experiment 1 were invited to participate in Experiment 3. Of the initial 62 participants, 56 students (50 females) aged between 19 and 22 ($M = 19.7$, $SD = 0.87$; years of education: $M = 13.1$, $SD = 0.58$) decided to take part in the modified task. None of the participants reported any neurological illnesses or conditions. All but two participants were right handed. All participants signed the informed consent form to participate in the study, which was approved by the Ethical Committee of the Faculty of Arts, University of Ljubljana.

Apparatus and materials
The apparatus and materials were the same as in Experiment 1, with the following exceptions. All the data were collected in the same experimental conditions. Specifically, the experiment ran on a Mac Mini computer (Intel Core 2 Duo processor with 2.0 GHz and 8 GB RAM) running Mac OS X 10.12 (El Capitan). Stimuli were presented on a 24” PC monitor screen (ASUS VG248QE, 1920 × 1080-pixel resolution; 60 Hz refresh rate). The participants were seated 55 cm from the screen.

Target stimuli were 35 px (1.08° visual angle) in length, with the main circle 19 px (0.59° visual angle) in diameter and the line 7 px (0.22° visual angle) wide. The invisible circle was 520 px (15.65° visual angle) in diameter. Placeholders and probe stimuli were 35 px (1.08° visual angle) in diameter, and the fixation point was 20 px (0.62° visual angle) in diameter.

Task and procedure
The task and procedure were the same as in Experiment 1, with the exception that no spatial pre-cue was shown before the presentation of the target stimuli, as indicated in Fig. 2.

Results

Absence of pre-cue does not reduce bilateral advantage
First, we checked whether an attentional pre-cue is crucial for inducing bilateral advantage. To test this we combined the data of matching participants from Experiment 1 and Experiment 3 and performed a 2-way repeated measures ANOVA with the factors of laterality (bilateral vs. unilateral) and pre-cue (absent vs. present). Note that for Experiment 1 only the data from participants who also took part in Experiment 3 (subset denoted as Experiment 1*, Fig. 4) were included in the analysis. The results showed a significant main effect of laterality, $F(1, 55) = 148.1$, $p < .001$, $η^2 = 0.177$, revealing significantly higher capacity for the bilateral ($K_b$) versus unilateral ($K_{uni}$) presentation of stimuli. Both the main effect of pre-cue, $F(1, 55) = 1.72$, $p = .195$, $η^2 = 0.004$, as well as laterality × pre-cue interaction, $F(1, 55) = 2.02$, $p = .161$, $η^2 = 0.003$, were not significant, suggesting that the presence of a pre-cue does not substantially affect the estimate of bilateral advantage (Fig. 4A).

Next, to fully replicate the analyses of Experiment 1, we tested the working memory capacity (CI_b) scores did not significantly differ from normal distribution, $W = 0.98$, $p = .348$, a one-tailed one-sample $t$-test was used to compare bilateral capacity index (CI_b) against 1 (full representational potential). The results revealed that in the absence of a pre-cue the bilateral capacity index remains significantly lower than 1, $t(55) = −4.36$, $p < .001$, $d = −6.83$, indicating that bilateral capacity does not reach the full bilateral representational potential (Fig. 5C).

Lastly, we computed a linear regression model to test whether representational potential (RP) is negatively associated with bilateral capacity index (CI_b). The absence of a pre-cue did not change the original finding of a significant decrease in bilateral capacity index (CI_b) with an increase in representational potential, $t(54) = −4.36$, $p < .001$, $β = −0.04$, $R^2_{adj} = 0.25$ (Fig. 7).

Discussion
The aim of the third experiment was to address the potential shortcomings of the first and second experiments. Specifically, our concern was that the design of the experiment allowed participants to direct their gaze towards the unilateral targets, which would enable their bilateral encoding and lead to the underestimation of bilateral advantage. The aim of this experiment was to replicate the initial findings by removing attentional pre-cues from the task paradigm, and consequently reducing the probability that the participants would shift their gaze from the fixation point and focus it on the target stimuli.

Though previous studies have indicated the importance of attentional pre-cues for inducing bilateral advantage (Holt & Delvenne, 2015), our results revealed not only that a significant bilateral advantage can still be observed in a working memory span task regardless of attentional pre-cue, but also that the results are essentially unaffected by the presence of a pre-cue.

The obtained results suggest that the participants in Experiments 1 and 2 did not move their gaze to the location indicated by the spatial pre-cue, and that the presence of a pre-cue does not affect the extent of the bilateral advantage. However, we should not dismiss alternative possibilities. One, that in Experiments 1 and 2 the participants did move their gaze, in effect reducing bilateral advantage, and that the absence of a pre-cue—though not completely removing it—also reduces the bilateral advantage to a comparable extent, resulting in no observable difference in the results between Experiments 1 and 3. This possibility is though unlikely, as the analysis showed no significant effect of pre-cue on the observed capacity and in the no pre-cue condition the observed capacities are actually numerically higher than in the pre-cue condition (see Fig. 4). The second possibility is that the duration of the target presentation afforded enough time for the participants in Experiment 3 to move their gaze and encode items bilaterally, resulting in both reduced bilateral advantage as well as no significant difference in the pre-cue versus no pre-cue conditions.

Though Experiments 1, 2 and 3 clearly demonstrate the existence of a bilateral advantage, the stricter control of eye movements—preventing bilateral encoding of unilaterally presented stimuli—and the use of a pre-cue—previously shown to be crucial for bilateral advantage (Holt & Delvenne, 2015)—could potentially further increase bilateral advantage to the point of reaching the full representational potential. Such results could support an alternative explanation to our conclusion that the capacity of visual working memory is limited by two systems. To test this possibility we designed an additional experiment in which we explicitly controlled the gaze position using an eye tracker.

Experiment 4
The results of the Experiments 1 and 2 suggested that the capacity of visual working memory is limited both by the ability to form independent visual representations as well as the ability for their active maintenance. However, we did not explicitly control for participants’ gaze. In Experiment 3 we omitted the spatial pre-cue to minimize the possibility of fixating gaze on the target items. The results replicated those of the first two experiments and additionally showed that the absence of a pre-cue does not affect the extent of bilateral advantage in the span task. The design though did not completely exclude the possibility that the participants did move their gaze after the presentation of the target items. Moving the gaze toward the target items would result in bilateral encoding of unilaterally presented stimuli, and therefore in underestimation of bilateral advantage. It could lead to the false conclusion that the bilateral advantage does not reach participants’ full representational potential, which is key support for the claim...
that the two systems limit the visual working memory capacity. To ensure that the participants did not move their gaze and instead fixated on the target items, and to estimate the effect of the pre-cue in a more controlled manner, we repeated the task both with and without a pre-cue while controlling for the participants’ gaze with the use of an eye-tracker.

Method

Participants
Sixty psychology and cognitive science students (56 females) aged between 19 and 31 ($M = 20.4$, $SD = 2.25$; years of education: $M = 13.6$, $SD = 1.19$) signed an informed consent form to participate in a 45-minute experimental session in which they completed both versions of the visual working memory span task (pre-cue present and pre-cue absent) while their eye-movements were tracked. All participants had normal or corrected to normal eyesight. None of the participants reported any neurological illnesses or conditions. All but four participants were right handed. For comparability, the sample size approximately matched those in Experiments 1 and 3. By participating in the experiment the students earned research credits that counted towards fulfilment of requirements for a course in cognitive psychology. The study was approved by the Ethical Committee of the Faculty of Arts, University of Ljubljana.

Apparatus and materials
The apparatus and materials were the same as in Experiments 1, 2 and 3, with the following exceptions. The experiment ran on a Mac Mini computer (3.6 GHz quad-core Intel Core i3 processor with 8 GB RAM) running 64 bit version of Windows 10. Stimuli were presented on 24" LCD screen (BenQ XL2420G, 1920 × 1080-pixel resolution; 60 Hz refresh rate).

To control for eye-movements, we used an EyeLink 1000 (SR Research, 2010) system. Gaze direction was calibrated using a nine-point calibration procedure. Gaze direction of the eye that allowed most reliable eye-tracking was recorded with a frequency of 1000 Hz. To ensure reliable eye-tracking, a stable head position, and constant 70 cm distance to the screen, the participants rested their chin on a fixed headrest. This resulted in slightly smaller visual angles of the presented stimuli compared to Experiment 3.

Target stimuli were 35px (0.78 visual angle) in length, with the main circle 19 px (0.42° visual angle) in diameter and the line 7 px (0.16° visual angle) wide. The invisible circle was 520 px (11.38° visual angle) in diameter. Placeholders and probe stimuli were 35 px (0.78° visual angle) in diameter, and the fixation point was 20 px (0.44° visual angle) in diameter.

Task and procedure
The participants completed both versions of the visual working memory span task: with pre-cue present and pre-cue absent. To avoid a possible training or fatigue effect, we alternated the order of the two versions across the participants.

To allow for control of the gaze during target presentation the task was adjusted in the following manner. First, at the start of the task the eye tracking parameters were set, the tracker was calibrated and the tracking accuracy validated. Next, during the presentation of the target stimuli and the delay before the response period, the position of the gaze was continuously monitored. If the gaze deviated from the central fixation point more than 100 px (2.22° visual angle), a red circle was shown in the middle of the screen for 500 ms, indicating a fixation break, and the trial was aborted. Aborted trials did not count towards computation of the span. Fixation breaks were triggered by saccades from the fixation point, blinks, as well as accumulated drift due to loss of accurate calibration. If the experimenter observed a drift in the accuracy of eye tracking, the task was paused to perform a drift correction, and—if necessary—repeat the calibration and validation procedure. By visual inspection of the proportion of aborted trials in both pre-cue present and pre-cue absent conditions we identified one participant as an outlier (64.6% of aborted trials in pre-cue present condition, Fig. S3), and excluded their data from all further analyses.

Results
Gaze control does not change bilateral advantage
First, we checked whether Experiment 4, in which we ensured that the participants held their gaze on the fixation point during target presentation, replicated the results obtained in Experiments 1 and 3. Specifically, we performed a 3-way mixed design ANOVA on the results of Experiments 1*, 3, and 4, with pre-cue (absent vs. present) and laterality (bilateral vs. unilateral) as within subject factors and gaze control (absent vs. present) as the between subject factor. The results revealed a significant main effect of laterality, $F(1, 113) = 215.8$, $p < .001$, $η^2 = 0.180$, reflecting significantly higher capacity for bilateral ($K_B$) versus unilateral ($K_{MIN}$) presentation of stimuli, as well as gaze control, $F(1, 113) = 21.7$, $p < .001$, $η^2 = 0.107$, reflecting overall lower capacities when eye fixation during target presentation was enforced. The main effect of pre-cue, $F(1, 113) = 1.27$, $p = .262$, $η^2 = 0.002$, was not significant, suggesting that the presence of a spatial pre-cue does not noticeably affect bilateral advantage (Fig. 4A). None of the interactions between main effects were significant (all $p > .578$).

Next, we tested whether the working memory capacity for bilateral presentation of targets measured in Experiment 4 reaches the participants’ bilateral representational potential. As $C_{IL}$ scores in the pre-cue present condition were not normality distributed, $W = 0.96$, $p = .038$, a Wilcoxon Signed-rank test was used to compare the bilateral capacity index ($C_{IL}$) against 1 (full representational potential). As the bilateral capacity index ($C_{IL}$) did not significantly differ from a normal distribution in the pre-cue absent condition, $W = 0.97$, $p = .115$, we used a one-tailed one-sample $t$-test. The results revealed that both with the presence, $V = 0$, $p < .001$, $d = −6.25$, and absence, $t(58) = −47.1$, $p < .001$, $d = −6.13$, of a pre-cue, the bilateral capacity index remains significantly lower than 1, confirming that bilateral capacity does not reach the full bilateral representational potential (Fig. 5D & E). Additionally, we checked whether bilateral capacity indices differ between pre-cue present and pre-cue absent conditions. A paired Wilcoxon Signed-rank test did not reveal significant differences, $V = 755.5$, $p = .441$, $d = 0.17$.

Lastly, to test whether the representational potential (RP) is negatively associated with the bilateral capacity index ($C_{IL}$) and investigate a possible interaction with the presence of a pre-cue, we computed a multiple linear regression model with the predictors of RP, pre-cue (present vs. absent) and their interaction. To test whether RP significantly predicted $C_{IL}$, we compared the models with and without inclusion of RP, which yielded a significant effect of RP, $F(114, 2) = 13.8$, $p < .001$, $β = −0.05$, $R^2_{adj} = 0.18$. To test the effect of the pre-cue, we compared models with and without inclusion of a pre-cue and found no evidence for an effect of a pre-cue, $F(114, 2) = 0.67$, $p = .513$, $β = −0.0002$, $R^2_{adj} < 0.01$. To test the effect of the RP × pre-cue interaction, we compared models with and without this interaction, and the results did not reveal a significant effect, $F(114, 1) = 0.28$, $p = .868$, $β = −0.003$, $R^2_{adj} < 0.01$. These results reflect a decrease in bilateral capacity index ($C_{IL}$) with an increase in the representational potential with no detectable effect of a spatial pre-cue (Fig. 7).

Fixation breaks
During task performance we recorded fixation breaks on average in 19.6% ($SD = 11.5$) of trials when a pre-cue was present and in 14.4% ($SD = 8.6$) when a pre-cue was not present. Specifically, fixation breaks during target presentation occurred in 5.7% of trials when a pre-cue was present and 4.6% of trials when a pre-cue was not present, whereas fixation breaks during the delay period occurred in 14.0% of trials.
when a pre-cue was present and 9.7% of trials when a pre-cue was not present.

We specifically focused on the question of whether the participants were more likely to break fixation for unilateral versus bilateral target presentation, and whether the presence of a pre-cue led to a higher probability of fixation breaks (Fig. S4). To answer these questions we focused on fixation breaks during target presentation only, as only these are relevant for ensuring unilateral versus bilateral target presentation and encoding. A 2-way repeated measures ANOVA with the factors of laterality (bilateral vs. unilateral) and pre-cue (absent vs. present) revealed no significant main effect of either pre-cue, $F(1, 58) = 1.15, p = .288, \eta^2 < .001$, or laterality, $F(1, 58) < .001, p = .983, \eta^2 < .001$, as well as no evidence of laterality × pre-cue interaction, $F(1, 58) = 0.374, p = .543, \eta^2 < .001$.

**Discussion**

The aim of the fourth experiment was to address the limitation of Experiments 1–3 by explicitly controlling for the participants’ gaze. Our concerns were that a gaze directed toward the targets instead of the centre of the screen would enable encoding of unilaterally presented stimuli. This would result in overestimation of unilateral capacity, underestimation of bilateral advantage and possibly the false conclusion that bilateral capacity does not reach full representational potential.

Controlling for the participants’ gaze, however, did not qualitatively change the results compared to Experiments 1 and 3. Regardless of the use of a spatial pre-cue, the capacities were higher when stimuli were presented bilaterally. Moreover, the bilateral capacity index did not reach the full representational potential. These results not only addressed the stated concerns, but also provided a second replication of the key findings in an independent sample of participants, jointly providing strong support for the proposition that visual working memory capacity is limited at two levels. Further exploration of the results also replicated the previously observed negative relationship between the bilateral capacity index and the representational potential both in the presence or absence of a spatial pre-cue.

Strict control of the participants’ gaze also enabled estimation of the effect of the pre-cue without a possible confounding factor of overt eye-movements. In contrast to the studies of bilateral advantage in change detection working memory tasks (e.g. Holt & Delvenne, 2014, 2015; for a review see Delvenne, 2012) that reveal a strong effect of attentional pre-cues and often found no effect of bilateral advantage without a presence of an attentional pre- or post-cue, our results consistently and conclusively show no appreciable effect of attentional pre-cuing on visual working memory performance or bilateral advantage on reconstruction of orientation in a working memory span task. A possible explanation for the differences between the experimental results could be that in studies where pre- or post-cues had a significant impact on the results the target stimuli were typically shown only briefly (150 ms), and the attentional cues were a pre-requisite for their efficient encoding. In contrast, the relatively long presentation time (500 ms) in our study gave the participants enough time to focus their attention and efficiently encode stimuli to effectively eliminate the need for and the effect of a pre-cue. Interestingly, additional analyses also revealed no evidence that the participants would be more likely to commit a fixation break when a spatial pre-cue was given.

Furthermore, the use of the eye-tracker resulted in overall lower estimates of VWM capacity, which could be ascribed to increased task difficulty as some of the attentional resources are diverted to maintenance of precise fixation and inhibition of blinks. This, together with possible frustration due to aborted trials even when participants made their best efforts to maintain fixation (e.g. due to blinks, drift in calibration or loss of reliable eye-track), could speak against the use of an eye-tracker, especially in populations that find the added burden of eye-tracking particularly taxing.

Overall, though only eye tracking can ensure unilateral target presentation and valid estimation of unilateral VWM capacity, our results suggest that—possibly due to the design of the task—the participants in Experiments 1–3 complied with the request to hold their gaze at the fixation point, even when their gaze was not explicitly controlled, indicating that the explicit enforcement of fixation might not be needed. As the presence of a pre-cue does not affect the results, and although we found no evidence that a pre-cue increases the probability of a fixation break, we would still recommend the omission of a pre-cue in a situation when either technical limitations or other considerations preclude the use of eye tracking.

**General discussion**

The first aim of this study was to directly investigate whether rather than reflecting a single limitation (e.g. limited focus of attention) (Cowan, 2005), working memory capacity might be, as suggested by Logie (2011), determined by the capacity of a number of systems that jointly enable representation, maintenance and manipulation of information. Specifically, we proposed that the capacity of visual working memory might reflect the capacities of two systems: a representational system, which enables establishment of a limited number of distinct visual representations, and an active maintenance system that enables sustained activation of all or some of the established representations in the absence of external stimuli, and protects them from possible distractors.

To test the proposed hypothesis we designed a visual working memory span task in which the participants were asked to maintain orientations of items that were presented to the left, right or across both visual hemifields. We reasoned that an increase in visual working memory capacity with the bilateral compared to unilateral presentation of items would indicate that each hemisphere functions as an independent representational system with limited capacity. Further, if in the case of the bilateral presentation of items visual working memory capacity does not reach the full representational potential of both hemispheres, we argue that this reflects a limitation of a second system necessary to maintain the representation of items established across the hemispheres.

Were the hypothesis to be confirmed, this would provide us with the possibility to obtain separate capacity estimates for the two systems limiting visual working memory capacity—in our model the representational and active maintenance systems—and enable us to explore how the two capacities change and interact throughout development and healthy aging, the second aim of this study.

To fulfil the two aims—first, to test and validate our model, and second, to explore the changes in the two proposed systems throughout development and healthy aging—we performed four experiments. In the following paragraphs the main findings and their implications will be discussed.

**Visual working memory capacity is limited by two systems, the ability to form visual representations and the ability for their active maintenance**

The results of all four experiments support the key proposition of the proposed model, namely that visual working memory capacity is limited by two systems. This conclusion is based on two observed results. First, the presence of bilateral advantage, and second, the fact that it fails to reach full representational potential. These results and their implications are discussed below.

First, we have shown that the participants performed better on a visual working memory span task when the items they had to encode and maintain were presented across both visual hemifields versus left or right visual hemifield only. The observed bilateral advantage is congruent with a number of previous studies (e.g. Delvenne, 2005; Holt & Delvenne, 2014, 2015; Umemoto et al., 2010; Zhang et al., 2017) showing that visual working memory performance is better when the
items to be remembered are distributed across both versus one visual hemifield. These results suggest that the left and right hemispheres have independent and limited abilities to establish visual representations, and that utilizing both can lead to better visual working memory performance. Importantly, this finding strongly indicates that the capacity of the visual working memory for orientations is limited at the level of the representational system.

To support this claim, alternative explanations need to be considered and addressed. Some potential explanations were addressed by the study design. Namely, by organizing the stimuli equidistantly in a circle we ensured that the spatial separation between the items was the same when they were shown across versus within a hemifield. Spatial separation therefore could not contribute to the observed differences in capacity in unilateral versus bilateral presentations. In a similar manner, it might be claimed that there is less interference between the items when they are encoded across the hemispheres versus within a hemisphere. However, rather than disputing that the representational system has a limited capacity, such an explanation would speak to the mechanism underlying the limitation.

Alternatively, it might be claimed (e.g. Holt & Delvenne, 2015) that it is easier to split attention—or another mechanism of maintenance—between hemispheres rather than within a hemisphere. In this view the properties of attention rather than the limited capacity of the hemisphere specific representational system would be the reason for the observed unilateral disadvantage. However, this alternative is hard to reconcile with the observation that across participants there are robust differences between the capacities observed when the items are shown to one or the other hemifield (Fig. 6). It would require one to posit the existence of separate limited capacity maintenance mechanisms or systems for left and right hemispheres. These would in turn become a part of the hemisphere specific representational systems themselves. Additionally, shifting the limitation from the level of representation to the level of maintenance would be in conflict with the finding of bilateral advantage in a stimulus tracking task (Alvarez & Cavanagh, 2005) in which the stimuli were presented throughout the tracking period, and so in principle required no mechanism of representation maintenance.

Second, we have shown that the bilateral advantage does not reach the full, joint potential of representational abilities of both hemispheres, i.e. bilateral representational potential. This finding can only be explained by the existence of a second source of limited visual working memory capacity. In our model, we have related the second source of limited visual working memory capacity to an active maintenance system that is required to maintain the representations established by the representational system. Though it is probable that additional mechanisms (some addressed in the limitations section) contribute to the observed inability to use the full representational potential, the limited ability to actively maintain visual representations in the absence of target stimuli is probably most widely accepted by the visual working memory literature.

These findings complement results of previous studies on bilateral field advantage. For example, Alvarez and Cavanagh (2005) demonstrated an almost twofold increase in capacity for tracking multiple objects when they were distributed across both versus a single hemifield. Consistent with a series of studies on the bilateral field advantage in working memory, our results, while clearly demonstrating bilateral advantage, showed a substantially smaller effect. However, this apparent discrepancy between bilateral field advantage in visual processing and working memory tasks naturally follows from the difference in the engagement of the purported active maintenance system. Namely, in Alvarez and Cavanagh (2005) the stimuli were presented throughout the tracking period, activating and updating the representations within the representational system and allowing the participants to make full use of the bilateral representational potential, when the tracked objects were distributed across both visual hemifields. In contrast, the visual working memory task in our and other studies requires sustained maintenance of representations in the absence of external stimuli, limiting the number of active representations—and with it the extent of bilateral advantage—to the capacity of the active maintenance system.

Together these results support the two key assertions of the proposed model: first, that visual working memory is limited by capacities of two systems—in our model a representational and an active maintenance system—and second, that whereas the representational system consists of two independent subsystems—one supported by the left and the other by the right hemisphere—there is a single active maintenance system that supports both representational systems. As suggested by Sander et al. (2012), this provides a novel framework for understanding the mechanisms of the formation and maintenance of information in the visual working memory.

Bilateral advantage differs across participants

The results of all three experiments show pronounced individual differences in the extent of their ability to make use of bilateral presentation of target items. The bilateral advantage varied from subjects that successfully utilize joint representational potential of the two hemispheres to those in which bilateral presentation does not provide any advantage in visual working memory task performance. Within the model explored in this study, the bilateral advantage reflects the relationship between representational potential—an estimate of the representational system’s ability to form independent representations of visual features—and bilateral capacity, an estimate of the active maintenance system’s ability to actively sustain representations of visual features in the absence of external stimuli.

The observed variability in bilateral advantage enabled further investigation of the basic assertion of the model, the relationship between the capacities of the two proposed systems, and the resulting bilateral advantage. The results showed a negative relationship between bilateral advantage and representational potential. This result is incongruent with the possibility that bilateral visual working memory capacity reflects a fixed proportion of the representational potential. Instead it indicates that the capacities of the representational and active maintenance systems—at least to some, significant extent—vary independently across participants, and that individuals with lower unilateral representational capacity have more free resources of the active maintenance system left to take advantage of bilateral representation, leading to higher observed bilateral advantage.

Working memory capacity changes with age

As with many cognitive abilities, visual working memory and its capacity develops at a young age, peaks in early adulthood and declines with aging (Brockmole & Logie, 2013). Studies have shown that specific cognitive abilities can peak at different times (Hartshorne & Germine, 2015) and change with different trajectories (Johnson et al., 2010). Using the ability to separately estimate the visual working memory representational and active maintenance systems’ capacities, we used our paradigm to explore their changes and interaction throughout the lifespan. We compared the results with the main theoretical positions and empirical findings, with a specific emphasis on healthy aging.

A decline in working memory has previously been identified as a characteristic of healthy aging (Braver & West, 2007; Park & Festini, 2017). As noted by Braver and West (2007), observations of a more pronounced decrease in working memory based on complex rather than simple measures of working memory, and coincident findings of significant differences in delay related activity in the prefrontal cortex (for a review see also Reuter-Lorenz & Sylvester, 2017), led many researchers to believe that whereas maintenance abilities and basic storage capacity are relatively spared, executive components of working memory are disproportionately affected. This led the research on working memory in aging to focus primarily on executive processes in behavioural research (e.g. Blair, Vadaga, Shuchat, & Li, 2011) and...
prefrontal cortex in cognitive neuroscience research (e.g. Rypma & D’Esposito, 2000).

Recently, though, Park and Reuter-Lorenz in their Scaffolding Theory of Aging and Cognition (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) propose that a disbalance in the observed impairments in maintenance and executive control components of working memory might be due to the first being compensated by the second, and the observed increase in prefrontal activation a reflection of this process. Relatedly, Sander et al. (2012) point out that differences in working memory performance through the lifespan are best understood as an interplay between top-down and binding processes, the first not yet fully mature until young adulthood and characterized by a marked decline with advancing age, and the second relatively mature in children, but still showing senescent decline in older adults.

Our study joins a number of recent efforts (Alloway & Alloway, 2013; Brockmole & Logie, 2013; Hartshorne & Germine, 2015; Rhodes et al., 2019) that address—as pointed out by Sander et al. (2012)—a significant lack of studies that would investigate both ends of the lifespan using the same paradigm. Specifically, our results show that the progression of change in the capacity of visual working memory is observed both in the capacity of the representational as well as the active maintenance systems. In contrast to findings by Sander et al. (2012) suggesting that representational potential might peak early and maintenance later in development, we have found both peaking at almost the same age and declining similarly in adulthood. Though not robustly different from the representational system’s capacity, active maintenance system’s capacity, however, seems to decline at a somewhat higher rate—a possibility that should be investigated further.

Importantly, though we have used a relatively simple visual working memory task that primarily depends on representation and maintenance processes (although see Section 6.5), we still observed a significant decline in performance in healthy aging. Together with recent studies e.g. showing a decrease in the resolution of visual working memory representations with age (Peich, Husain, & Bays, 2013) and a decline in representational capacity (Souza, 2016), these results, especially the robust decline in the capacity of the representational system capacity, suggest that broader research on working memory in aging beyond the currently predominant focus on executive components and prefrontal cortex is merited.

Relevance and open questions

To the best of our knowledge, this is the first study focusing on direct evidence that the capacity of the visual working memory is limited by two systems, purportedly a system that supports the establishment of independent visual representations and a system for their active maintenance in absence of external stimuli, and showing that both systems’ capacities change throughout development and healthy aging.

The data obtained challenge some of the leading models of visual working memory. To address the disparity we proposed a conceptual model that explicitly integrates the obtained results. In this section we review how the proposed model and the obtained results relate to existing models of working memory and implicated brain systems.

Multicomponent model of working memory

As explicitly stated by Logie (2011), the multicomponent model of working memory proposes that the limited capacity of the working memory arises as an emergent phenomenon of multiple interactive systems of limited capacity. The specific nature of limitation is though not always clear or explicitly stated. Here we propose that in the case of visual working memory the limitation is both in the number of individual representations that can be established, which are independent for each hemifield, as well as the number of representations that can be actively maintained.

The dual limitation matches well with the proposed interaction between the limited capacity visual cache that holds visual codes, and the limited capacity inner scribe tasked with refreshing (Logie, 2011). A few challenges and questions persist, though. First, based on a careful review of multiple studies (Logie & Van Der Meulen, 2009) the visual cache is currently envisioned as a unitary system that is distinct from early phases of visual processing and visual imagery, the latter supported by the visual buffer as envisioned by Kosslyn (2005). Specifically, the visual cache is proposed to store visual codes that are either mapped from long term memory or result from thorough perceptual processing of visual input. Such a specification of the visual cache is not congruent with the demonstrated hemispheric specific independent representational systems.

In line with Logie (2011), the visual sensory information presented to either hemisphere should undergo full perceptual processing and be stored as abstracted visual codes in a unitary visual cache, which, however, does not leave room for bilateral advantage. To allow for bilateral advantage the model would need to be extended to allow separate visual caches for the two hemispheres. Given that the visual cache holds processed visual codes that can be generated from sources other than visual input, this seems unlikely.

An alternative possibility to explain bilateral advantage within the current conception of the visual cache would be that the transfer of visual information to, and their encoding within, the visual cache is made more efficient when transferred in parallel from two separate visual perceptual systems. Given the relatively long display of visual targets (500 ms) and lack of demonstrable effect of attentional pre-cuing, this explanation seems unlikely as well. It could, however, be explored empirically by changing the duration of target displays.

The second question pertains to the potential role of the episodic buffer. The episodic buffer was envisioned (Baddeley, 2000, 2012) to enable storage of bound multidimensional information and its access to conscious awareness. Recently (e.g. Allen, Baddeley, & Hitch, 2006; Allen, Hitch, Mate, & Baddeley, 2012, for a review see Baddeley, Allen, & Hitch, 2011) it has been mostly explored in the visual domain, binding individual visual features (such as colour and shape), which are primarily stored in the visuo-spatial sketchpad. As in this study only a single visual feature (orientation) had to be maintained in working memory, it is unclear whether engagement of the episodic buffer would be required. This could be explored by using multiple bound and unbound features in future studies. However, as visual information reaches the episodic buffer through the visuo-spatial sketchpad (Alan Baddeley, 2012), the dilemmas related to the visual cache remain.

State-based models of working memory

As presented in the introduction, state-based models (e.g. Cowan, 2005) propose that the capacity of the working memory, operationalized as the focus of attention, is limited only by attentional resources controlled by the central executive or pulled by automatic orienting responses. If that were the case, no bilateral advantage should be observed. We see two possible explanations within state-based models. The first is proposed by Holt and Delvenne (2015), who—citing multiple sources—suggest “that the focus of attention can be split to non-contiguous locations more easily when the locations are divided across hemispheres relative to within a hemifield” (p. 55). This explanation would keep limited attentional resources as the only source of limited working memory capacity. We see two problems with this explanation. First, as discussed in the previous section, the bilateral advantage obtained in previous studies often seems to rely on attentional pre-cuing, which enables encoding of only briefly presented visual items (Holt & Delvenne, 2015), whereas in our study no effect of pre-cuing is observed. The second, and more problematic, issue with this explanation are the observed differences in the unilateral capacity between the two hemispheres observed in all experiments (see Fig. 6). As the items and their arrangement were the same when displayed to the left or right hemispheres, it is difficult to explain why attention would be easier to divide within one versus the other hemisphere. A more
parsimonious explanation is that the two hemispheres support independent representational systems with limited capacity that varies between them.

The second alternative is related to the statement that the activation of the relevant representations “is limited only by interference effects and possibly the passage of time” (Cowan, 2005, p. 42). As the passage of time was equal in the unilateral and bilateral presentations of items, the bilateral advantage could then only be ascribed to stronger interference within than between visual hemifields. In relation to our conceptual model and results, the limitation of the representational system would then stem from item interference. The same question remains, though: why would interference be more debilitating in one versus the other hemifield and the related representational system? Again, in our opinion the more parsimonious explanation is that the representational system itself is of limited capacity in the ability to form distinct representations, and that the specific capacity may differ between the two hemispheric representational systems. Interference though can be a candidate mechanism for limited representational system capacity, and this possibility should be explored further.

The issue of the specific source of limitation—interference versus ability to form independent representations—could possibly be resolved by exploring to what extent the unilateral capacity is affected by the distinctiveness of the items to be remembered. If the key limitation is interference, then unilateral capacity should increase to the point of matching bilateral capacity with more distinct items, and conversely unilateral capacity should decrease and bilateral advantage increase with reduced distinctiveness between the items to remember. If the key limitation is the ability to form independent representations, then the bilateral advantage should remain constant with changes in item distinctiveness. Though the experiment was not optimal with regard to addressing this question, Holt and Delvenne (2015) (Experiment 2) failed to obtain a bilateral advantage with a decrease in item distinctiveness (colour contrast), despite a significant effect on overall performance—a finding more congruent with a limited ability to form independent representations.

An additional support for limited capacity representational system and a challenge for the focus of attention as the single source of limitation comes from the previously cited study by Alvarez and Cavanagh (2005). Their study showed that even when visual objects are present and can directly activate their representations in the representational system, the unilateral capacity to track them is significantly below the bilateral capacity, which indicates an inherent limitation with regard to the number of objects that can be concurrently represented in the representational system, irrespective of attentional limitations. Additionally, the disparity between bilateral advantage in visual tracking versus working memory indicates that different resources are engaged in the two cases. One possibility is that a visually presented object can directly become part of the focus of attention—a possibility that goes against much evidence on the accessibility of unattended objects (for a review see Cowan, 2005). Another possibility is that—similar to the assumptions of the multicomponent model of working memory—active maintenance of visual objects is separable from the central executive attentional resources.

**Implicated brain systems**

Though our study provides behavioural evidence of two limits to visual working memory, it does not provide information about their neuroanatomical substrate. Based on previous studies and the literature (Eriksson et al., 2015; Nee et al., 2013; Riggall & Postle, 2012; Sander et al., 2012) we can, however, speculate that what we describe as representational and active maintenance systems reflect the function of posterior and prefrontal brain regions, respectively. The representational system would include posterior regions that are responsible for early processing of visual information and their encoding by establishing their neuronal representations that are retained when the information is no longer present in the external environment. As sustained activity of the neurons coding for a specific visual representation in posterior regions is needed for the representation to survive the retention period, a second, active maintenance system, is engaged. This system depends on top-down processing most often associated with frontal brain areas (Eriksson et al., 2015; Liang, Liu, & Hu, 2016; Nee et al., 2013) that with their recurrent loops support ongoing activation of the representations established in the representational system in the absence of the external stimuli and protect them from possible distractors.

Though widely accepted (e.g. Eriksson et al., 2015; Reuter-Lorenz & Park, 2014; Riggall & Postle, 2012; Sander et al., 2012), as recently discussed by Christophel, Klink, Spitzer, Roelfsema, and Haynes (2017) the distinction between the roles of prefrontal and posterior regions might not be that clear. Many studies (for a review see Christophel et al., 2017) jointly suggest that information held in working memory can be represented by one or more of a widely distributed network of regions—including the prefrontal cortex—supporting representations at different levels of abstraction. Due to the nature of the task, and the observed bilateral advantage indicating the use of independent lateralized representational systems, we argue that the visual information required to perform the task in our study was most likely represented in posterior visual brain areas. Based on the proposal by Christophel et al. (2017), however, we would predict that the bilateral advantage might not be observed in studies in which the participants find it advantageous to represent the information to be maintained in a more abstract form.

Additionally, while present in other literature (e.g. Eriksson et al., 2015), a division between representation and maintenance processes is currently absent in the proposal by Christophel et al. (2017). Whereas our finding of strong support for the engagement of two systems that jointly limit visual working memory capacity is most easily mapped to the representation of information and its active maintenance, the results could be reframed as reflecting a difference in the capacities of two systems representing and maintaining information at different levels of abstraction, both necessary for successful completion of the task. Further insights to differentiate between these possibilities could be gained by future brain imaging studies.

**Utility and limitations**

Enabling separate capacity estimates of the representational and active maintenance systems, the lateralized visual working memory span paradigm developed for this study provides a novel and useful tool in the exploration of the two working memory systems and their interactions not only in research on healthy aging, but also on disease. As working memory is most often among the first abilities to be impaired in many neurodegenerative (Bublak et al., 2002) and neuropsychiatric (Goldman-Rakic, 1994) diseases, more specific information on which component is primarily affected in individual diseases, and how the interaction between the two systems changes as a disease progresses, could assist in better understanding of the disease, its prevention, diagnosis and treatment.

When evaluating the obtained results as well as the potential of the paradigm for its use in other settings, the specific nature and complexity of the task needs to be considered. Specifically, in comparison with other paradigms used to measure visual working memory capacity, e.g. change detection or item recognition tasks in which the participant only compares the items held in memory with the presented probe stimuli (Rouder, Morey, Morey, & Cowan, 2011), the participants in our study had to reconstruct the previously presented items, a task that requires maintenance of the content of visual working memory in the face of novel visual stimulation and processing, engaging inhibition and related executive processes to a larger extent than a “simple” maintenance task. From this perspective the task might be regarded as closer to complex than simple span tasks, and at least some of the limitation ascribed to the active maintenance system could be related to the
second factor of executive control, as described by Engle and Kane (2003). In a similar manner, the limitation ascribed to the active maintenance system could to some extent be ascribed to response interference.

Whereas these considerations do not undermine the key finding of two limits to visual working memory, they jointly highlight the need to better understand the specific contributions to the observed limits of the purported active maintenance system. Additional research should help discern whether they are to be considered as constituent processes of the active maintenance system and its limitation, or rather as additional working memory independent sources of interference resulting in underestimation of the active maintenance system, the observed bilateral capacity of visual working memory and related bilateral capacity index, an indicator of bilateral field advantage.

Further, in our study, specifically due to the fact that the orientations had to be reconstructed in the correct locations, we tacitly considered that the items to be recalled were held in the working memory as visual objects and not only as individual features. As the task required no other binding than that of a single visual feature (orientation) to a specific location, this, however, might not have been the case. Therefore, an open question remains as to whether a larger capacity for single features might be obtained if the specific location was not important, and whether the results might be different if the task required the participant to maintain and report objects that included additional (e.g. colour-shape) binding. Addressing these questions will be the focus of future research.

Lastly, though the presented findings are stable and were replicated over four experiments with different samples, it has to be acknowledged—as indicated in previous paragraphs—that they currently pertain to a single visual feature (orientation) and task paradigm. They need to be extended with additional research to explore other visual features (e.g. colours and shapes) as well as other factors (e.g. response interference) determining the observed results.

Conclusions

In this study we have shown that visual working memory capacity is limited by two systems, purportedly a representational system consisting of two independent stores tasked with forming distinct representations of visual objects, and a unitary active maintenance system enabling their sustained activation in absence of external stimuli. This finding supports novel perspectives in theoretical debates, offers alternative interpretations of existing empirical data and invites future research. Moreover, investigation of the two systems across lifespan revealed significant developmental and aging changes in both systems. Despite a slight indication that the active maintenance system might decline faster in aging, this finding emphasizes the need to widen the research on working memory in healthy aging from the predominant focus on executive components to also consider a decline in the ability to form representations of items to be held in working memory.

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CRedit authorship contribution statement

Anka Slana Ozimič: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Project administration, Visualization, Writing - original draft, review & editing. Grega Repovš: Conceptualization, Methodology, Data curation, Software, Supervision, Visualization, Writing - original draft, review & editing, Funding acquisition.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jml.2020.104090.

References

Allen, R. J., Baddeley, A. D., & Hitch, G. J. (2006). Is the binding of visual features in working memory resource-demanding? Journal of Experimental Psychology: General, 135(2), 289–315 https://doi.org/10/b58k5.
Allen, R. J., Hitch, G. J., Mate, J., & Baddeley, A. D. (2012). Feature binding and attention in working memory: A resolution of previous contradictory findings. Quarterly Journal of Experimental Psychology, 65(12), 2369–2383 https://doi.org/10/geb8j.
Alloway, T. P., & Alloway, B. G. (2013). Working memory across the lifespan: A cross-sectional approach. Journal of Cognitive Psychology, 25(4), 84–93 https://doi.org/10/ggb8j.
Alvarez, G. A., & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemispheres. Psychological Science, 16(8), 637–643 https://doi.org/10/0/bnx8b.
Baddeley, A. (1996b). Exploring the central executive. The Quarterly Journal of Experimental Psychology Section A, 49(1), 5–28 https://doi.org/10/c86bb8.
Baddeley, A. (1996c). The fractionation of working memory. Proceedings of the National Academy of Sciences, 93(24), 13968–13972 https://doi.org/10/d67wm.
Baddeley, A. (2000). The episodic buffer: A new component of working memory? Trends in Cognitive Sciences, 4(11), 417–423 https://doi.org/10/dtmnh.
Baddeley, A. (2012). Working memory: Theories, models, and controversies. Annual Review of Psychology, 63(1), 1–29 https://doi.org/10/e658j.
Baddeley, A., Allen, R. J., & Hitch, G. J. (2011). Binding in visual working memory: The role of the episodic buffer. Neuropsychologia, 49(6), 1393–1400 https://doi.org/10/gdb8j.
Baddeley, A., & Hitch, G. J. (1974). Working memory. In G. A. Bower (Vol. Ed.), Recent advances in learning and motivation: Vol. 8 (pp. 47–89). https://doi.org/10/1016/s0079-7421(08)60452-1.
Bragard, T. (2012). Calculating and graphing within-subject confidence intervals for ANOVA. Behavior Research Methods, 44(1), 158–175 https://doi.org/10/bq9d3.
Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1), https://doi.org/10.18637/jss.v067.i01.
Bettencourt, K. C., & Xu, Y. (2016). Decoding the content of visual short-term memory under distraction in occipital and parietal areas. Nature Neuroscience, 19(1), 150–157 https://doi.org/10/g79bb.
Blair, M., Vadaga, K. K., Shuchat, J., & Li, K. Z. H. (2011). The role of age and inhibitory efficiency in working memory processing and storage components. Quarterly Journal of Experimental Psychology, 64(6), 1157–1172 https://doi.org/10/fm34d3.
Braver, T. S., & West, R. (2007). Working memory, executive control, and aging. In P. I. M. Craik, & T. A. Salthouse (Eds.), The handbook of aging and cognition (3rd ed.). https://doi.org/10.4324/9780203837665.ch7.
Brockmole, J. R., & Logie, R. H. (2013). Age-related change in visual working memory: A study of 55,751 participants aged 8–75. Frontiers in Psychology, 4, 1–5 https://doi.org/10/gdz7v2.
Buer, R., & Sicalquin, J.-C. (1998). The visuospatial sketchpad for mental images: Testing the multicomponent model of working memory. Acta Psychologica, 98(1), 17–26 https://doi.org/10/c0x85.
Bublik, P., Müller, U., Gron, G., Reuter, M., & von Cramon, D. Y. (2002). Manipulation of the left and right visual hemifields. Journal of Cognitive Psychology, 14(11), 417–423 https://doi.org/10/d4tmmh.
Cowan, N. (1995). Attention and memory: An integrated framework. Retrieved from DOI: 10.1093/acprof:oso/9780195119107.001.0001.
Cowan, N. (2010). The magical mystery four: How is working memory capacity limited, and why? Current Directions in Psychological Science, 19(1), 51–57 https://doi.org/10/bfsc5.
Cowan, N. (2005). Working memory capacity (1st ed.). Retrieved from http://dx.doi.org/10.4324/9780203342398.
D’Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory.
