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The revolution of resolution in visual working memory: Insights into goal-directed behaviour from the delayed-estimation task

Thesis Booklet

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Introduction and main objectives

Goal-directed behaviour relies on the orchestration of multiple different cognitive processes, and working memory (WM) is the theoretical construct that is considered to be responsible for the temporary and active maintenance of information needed for the execution of behavioural responses (Baddeley, 1986; Miyake & Shah, 1999). The required information ranges from the past experiences and intentions to the most recent sensory inputs, also including interim results of mental operations, action plans, and task rules. WM plays a crucial role in a wide variety of – if not all – cognitive tasks, and its disturbance can be observed in different clinical conditions (Baddeley & Hitch, 1974; Budson & Price, 2005; Goldman-Rakic, 1992; Grover et al., 2021), and also as a function of ageing (Salthouse et al., 1989). Therefore, the thorough investigation of WM is of critical importance, not exclusively to satisfy the scientific curiosity about how the brain works, but also to make enormous steps toward the early detection and treatment of the conditions when WM function gets compromised.

Visual working memory (VWM) is responsible for the short-term maintenance and manipulation of visual information, and one outstanding question of the past decade has been concerned about the amount of information VWM is capable of retaining (Luck & Vogel, 2013; Olivers & Van der Stigchel, 2020). Two lines of concepts emerged, one stating that information is stored in a limited number of chunks, and the other suggesting that a limited resource can be distributed among an unlimited number of memoranda. According to the former view (slot-based theories), VWM can maintain information about approximately 3 to 4 objects in full complexity, while objects above this limit are not remembered at all (Luck & Vogel, 1997, 2013). Evidence in favour of this framework mostly derives from tasks applying discrete and easily distinguishable stimuli and binary responses, for example change-detection tasks, where participants need to indicate whether the initial display of stimuli (e.g. coloured squares) has changed at the repeated presentation or not (Ma et al., 2014). In spite of the long-lasting prominence of this view, the question remained: Does cognition indeed operate in such an all-or-nothing fashion?

The delayed-estimation – or continuous report – task is an increasingly popular paradigm used in VWM research for the assessment of memory function in a more precise way than the more traditional recognition tasks. In a delayed-estimation task, the participant is instructed to memorise some (one or more) properties of different objects (e.g. their colour), and following a retention interval, report the value of the cued object’s memorised property on a continuous scale (e.g. by clicking on the remembered colour on a colour wheel). While a recognition task requires a yes or no decision from the participant, the delayed-estimation task – given its continuous nature – has the potential of providing high-resolution information of the participant's memories (Bays et al., 2009; Gorgoraptis et al., 2011; Zhang & Luck, 2008). The advent of the delayed-estimation task (Wilken & Ma, 2004) and its clever utilisation (Bays et al., 2009; Zhang & Luck, 2008) gave rise to the resource-based class of models, capturing VWM capacity as a limited but freely distributable resource. With the increasing number of items to be remembered, the resource has to be divided between more and more items, resulting in a smaller share at higher set sizes, and ultimately, in weaker performance. The use of continuous reporting not only enabled the assessment of the quality of the VWM representations, but also inspired a variety of models offering explanations why VWM performance gets compromised. The current doctoral work is centred around this highly-influential task, and how it brings science closer to the comprehension of goal-directed behaviour.

The aim of the present doctoral work was threefold: First, to demonstrate that WM forms an integral part of human cognition, by establishing new experimental evidence on its connection with attention, long-term memory and the motivational system, raising the importance of complex, multidomain approaches when investigating cognition. Second, to demonstrate the potential in experimental tasks providing precise measurements of the most subtle but significant cognitive processes, and how these tasks could be exploited to notice and track pathological changes in cognition. Third, to demonstrate that along with the most state-of-the-art scientific advances, means simple as motivation can be utilised to achieve better cognitive performance subserving goal-directed behaviour. Contrary to the traditional span, n-back, delayed match-to-sample and change-detection tasks predominantly used in WM research, the delayed-estimation task provides a wealth of high-resolution information on the quality of WM representations. This high-resolution information derived from the delayed-estimation task has been utilised to achieve these goals, adding solid and valuable new evidence to our existing knowledge on how WM works.

Thesis point I. Top-down attentional control and the mitigation of interference between competing working memory representations are closely related functions.

Related article:

Study 1: Hermann, P., Weiss, B., Knakker, B., Madurka, P., Manga, A., Nárai, Á., & Vidnyánszky, Z. (2021). Neural basis of distractor resistance during visual working memory maintenance. *NeuroImage*, *245*, 118650.

Considering the limited capacity of VWM, the effective filtering of the endless flow of information is of critical importance (Chun et al., 2011; Myers et al., 2017). Thus, an intriguing question is what determines the subset of stimuli reaching VWM. Attention is thought to play a pivotal role in this. As Desimone and Duncan (1995) pointed out in their influential biased competition model, external visual stimuli are competing to be represented by the brain, and attentional signals are capable of biasing this competition, by prioritising either stimuli with salient visual properties (such as high contrast), or stimuli that are relevant in goal attainment. While stimulus saliency has a bottom-up impact on the system, task-relevance is conveyed by top-down attentional templates, likely originating from the brain areas also involved in WM. Importantly, as the internal representations have the authority to modulate perception, external stimuli are also capable of influencing the selection of WM-content when the content and the external stimuli have matching features. Thus, the visual percept, and the success of the goal-directed behaviour both depend on the result of computations integrating this bidirectional modulation (Hollingworth et al., 2008; Serences & Yantis, 2006; van Ede et al., 2020). Along with the selection of stimuli, goal-relevant VWM representations also need to be protected from intrusive external input and the ability to suppress distracting information is thought to play an indisputably important role in cognition, as suggested by the correlation between distractor-resistance and WM capacity (McNab & Dolan, 2014; Postle, 2006; Vogel et al., 2005). Distractor-resistance is especially challenging, when the distractors share common visual properties with the to-be-remembered objects (Mallett et al., 2020; Rademaker et al., 2015). Besides external irrelevant stimuli, WM maintenance is also challenged by its own content: item representations are compromised by each other, a phenomenon being referred to as interference. When items are presented sequentially rather than simultaneously, serial position biases can be observed in the recall performance, with proactive interference protecting the first as compared to the later stimuli in a sequence, and retroactive interference where the earlier representations are being disrupted by subsequent processing (Dewar et al., 2007; Keppel & Underwood, 1962). On the Sternberg task (1966) – which can be considered as the prototype of the previously introduced delayed match-to-sample and therefore also the delayed-estimation tasks – large recency, and modest primacy effects were found (Oberauer, 2003) leading to the suggestion that earlier items in the sequence are more severely affected by interference, with items in the middle experiencing the most adverse effects.

To summarise the previously introduced theories and results, overcoming both the detrimental effects resulting from the interference between relevant memoranda and the distraction posed by irrelevant external stimuli seem to be crucial in successful VWM performance. Study 1 (Hermann et al., 2021) provided an excellent opportunity to bring these two, generally distinctly discussed aspects of forgetting together. Participants of Study 1 completed a delayed match-to-sample task, where they were instructed to maintain compound images of faces and gratings. The category of the to-be-remembered object was cued retrospectively following the memoranda, and in the delay period of the trial, irrelevant distractor images matching to or differing from the memorandum category appeared. The neural responses to the congruent and incongruent distractors were monitored using electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) in two data acquisition sessions, on the same participants. The results showed that the processing of congruent delay distractors is mediated by two control mechanisms with opposing effects. On the one hand, distractors matching the WM content were automatically prioritised, reflected by the enhanced processing of distractors matching the WM content. On the other hand, congruent face distractors also triggered the reactive allocation of attentional resources, to protect the WM content from the interference posed by the irrelevant distractor items.

More importantly, the same participants also completed a delayed-estimation task with consecutively presented bars with different colour and orientation. Crucially, since participants were not informed in advance of the identity of the test item, they had to maintain all three bars. Participants were instructed to report the orientation of the bar marked by the colour of the probe as accurately as possible. The results indicated that the precision with which an orientation is recalled, correlates significantly with the behavioural distractor resistance measured in the delayed match-to-sample task. In the EEG data acquisition session, the strong association between the behavioural distractor resistance and orientation recall precision was dominated by the case when the second bar was tested in the delayed-estimation task. The behavioural data of the fMRI session showed that the recall precision for the first and second list positions both correlated significantly with distractor resistance. These results are in line with the notion that higher effort is needed for the successful maintenance of earlier items in a sequence since those items are more prone to interference. Furthermore, Study 1 also demonstrates that the ability to resist irrelevant external distractors is strongly associated with the capacity to overcome interference between relevant items in the VWM.

Thesis point II. Shared feature binding processes underlie the formation of coherent visual working memory and long-term object memory representations.

Related articles:

Study 2: Manga A., Havadi-Nagy M., Székely O., & Vidnyánszky Z. (2021). Demencia prevenció: A korai diagnózistól a személyre szabott intervencióig. *Scientia et Securitas, 2*(2), 207–219.

Study 3: Manga, A., Madurka, P., Vakli, P., Kirwan, C. B., & Vidnyánszky, Z. (2021). Investigation of the relationship between visual feature binding in short- and long-term memory in healthy aging. *Learning & Memory, 28*(4), 109–113.

Experimental tasks such as the delayed-estimation paradigm collecting high-resolution information have enormous potential in noticing even the most subtle alterations in goal-directed behaviour, therefore could be exploited in the early detection of pathological changes in cognition. While some cognitive functions remain relatively intact, others such as WM and long-term episodic memory are known to be profoundly affected not only in healthy ageing, but in pathological ageing processes as well (Arvanitakis et al., 2019; Hedden & Gabrieli, 2004). The early diagnosis of dementia is a crucial yet challenging task, as the patients ask for medical help too late, when dementia is already fully developed. This is because the cognitive decline is usually noticed only at this late stage of the disease, which is however preceded by a long period of covertly thriving neuropathological changes (Mortamais et al., 2017). In Alzheimer's disease (AD), the underlying biological pathologies are present decades before the cognitive symptoms unfold (Firth et al., 2020; Ritchie et al., 2017), suggesting that the early detection of the disease would be possible with screening programs targeting the behavioural outcomes and/or their biological underpinnings by using sensitive and non-invasive tools. Study 2 (Manga, Havadi-Nagy, et al., 2021) was written with the aim of giving a comprehensive yet thorough picture of the symptoms, course, diagnosis and outcomes of dementia, especially due to AD. The review characterises the neural changes associated with the disease and their assessment via brain imaging techniques, moreover summarizes the recent technological advances of biomarker research. Since the exact aetiology of the disease is unknown, and the progression-reversing medication is lacking, the importance of early detection stands in the focus of the review, strongly emphasizing the role of prevention and intervention in preserving longevity. A crucial step in facilitating the development of early detection methods would be to know precisely what to detect. Therefore, the definition and characterisation of those cognitive mechanisms that are affected the most by ageing would be a key in developing the most sensitive cognitive assessment methods, with the retention of associative information being a promising candidate for this purpose.

Despite the crowd of different dimensions and feature values, objects are perceived and treated as coherent, meaningful wholes (Fougnie & Alvarez, 2011), inferring the presence of a binding mechanism responsible for the connection of the different object properties (Reynolds & Desimone, 1999). The understanding of bound representations profited greatly from the advent of continuous adjustment tasks, providing high-resolution information about the stored objects. By using this task, it has been identified that in addition to the variability of mnemonic precision (the standard deviation of a normal distribution centred at the target object's value) and random guessing, the misbinding of object features also accounts for a substantial portion of VWM recall errors (Bays et al., 2009).

WM is not an exclusive property of the mind challenged by stimulus complexity: long-term episodic memory (Tulving, 1972, 2002) also relies on bound, coherent representations. Episodic memories comprise several elements of different dimensions and modalities that need to be connected to form meaningful events (Ekstrom & Yonelinas, 2020; Ranganath, 2010; Rolls, 2013). As memoranda sharing features with each other are prone to interference, successful remembering also requires the careful discrimination between the different yet highly overlapping information (O'Reilly & McClelland, 1994; Yassa & Stark, 2011). Supporting early computational theories and rodent studies, the central role of the hippocampus in mnemonic discrimination has been demonstrated by the Mnemonic Similarity Task (MST) (Bakker et al., 2008; Kirwan & Stark, 2007). Computational theories assume, that along with keeping the different events distinguishable, the hippocampus is a key structure in creating unitary representations of an episode via rapidly and automatically formed conjunctions between the stimulus features when attending to the environment (Kesner & Rolls, 2015; O'Reilly & Rudy, 2001; Ranganath, 2010). While the fundamental role of the hippocampus in episodic long-term memory appears to be well-established, some papers have suggested that the hippocampus and the surrounding medial-temporal lobe cortex is also involved in the creation of novel representations in the case of short-term retention (Gilbert et al., 1998; Jonides et al., 2008; Opitz, 2010). In spite of the notion that this line of research would benefit greatly from empirical studies assessing short-and long-term memory function in the same participants, the number of studies obtaining both measures of episodic memory discrimination and WM performance is scarce. A few papers reported WM scores measured on the digit span task in addition to the MST (Bennett et al., 2019; Bennett & Stark, 2016; Venkatesh et al., 2020), and found that behavioural discrimination and WM loaded onto distinct factors (Bennett & Stark, 2016). It is important to note however, that the digit span task provides a coarse and quantal measure of WM (Yonelinas, 2013; Zokaei & Husain, 2019), moreover, the relationship between pattern separation processes in long-term memory and WM binding was not previously explored.

Study 3 (Manga, Madurka, et al., 2021) aimed at filling this gap by measuring both behavioural discrimination and the quality of VWM representations. Behavioural discrimination was assessed by the object version of the MST (Stark et al., 2013, 2019), while the previously described orientation delayed-estimation task was used to measure the resolution of VWM (Gorgoraptis et al., 2011), in a large sample of older adults. Computational modelling was applied to decompose errors committed on the delayed-estimation task (Bays et al., 2009; Suchow et al., 2013), and estimate the participants' performance on the retention of bound information. The findings of Study 3 showed that behavioural discrimination is related to the successful formation of coherent VWM representations in old age: discrimination correlated significantly and negatively with the probability of reporting the orientation of a non-target feature, meaning that the preserved ability to discriminate between similar objects in long-term memory is associated with the reduced probability of misbinding in VWM. Critically, no such correlation was found between the discrimination and the variability and guessing parameters of the employed model, ruling out the possibility of a general connection between the two tasks.

All things considered, Study 3 provides important novel insights into the still debated question that episodic memory and working memory may have common neural mechanisms (Lugtmeijer et al., 2021). The shared neural mechanism underlying both successful short-and long-term memory performance is suggested to be the binding of multiple disparate features, with the hippocampus as a candidate neural substrate of this binding process (Cabeza et al., 2002; Fallon et al., 2016; Lee & Jung, 2017; Olsen et al., 2012). While the investigation of the effect of healthy ageing on the maintenance of bound information in WM provided mixed results so far, literature started to converge on the view that instead of typical ageing, binding problems might signal pathological processes (Schneegans & Bays, 2019; Zokaei & Husain, 2019). These results make the delayed-estimation task providing information about feature conjunctions a promising tool for the early assessment of pathological age-related changes. The question can be raised however what the significance of early detection is, and whether any steps can be taken to counteract the effects of healthy and pathological ageing processes. Engaging the relevant cognitive networks via various intervention methods such as cognitive training and psychosocial stimuli forms an important part of the research on counteracting the effects of ageing, with old roots (e.g., Baltes & Lindenberger, 1988) and ever increasing popularity. However, a still debated question is whether cognitive performance could be indeed truly enhanced (Brem & Sensi, 2018). Considering that the basic principle of any intervention is the regular and devoted participation in the assigned activities, it is reasonable to assume that motivation might play a role in the success of the different training programmes (Brem & Sensi, 2018). Abundant literature has investigated the neural basis and effects of motivation on a wide range of cognitive functions, looking for answers for the intriguing questions whether cognitive processing per se or the inner drive to exert effort gets compromised in ageing, and whether incentives could be utilized to restore or even enhance cognitive performance.

Thesis point III. Model parameters and reaction time derived from the delayed-estimation task are sensitive markers of the motivation-working memory interaction, and demonstrate that the motivating effect of incentives is present in young and old age as well.

<u>Related article:</u>

Study 4: Manga, A., Vakli, P., & Vidnyánszky, Z. (2020). The influence of anticipated monetary incentives on visual working memory performance in healthy younger and older adults. *Scientific Reports, 10*(1), 8817.

Each action has an outcome, and motivation can be defined as the impact of this outcome on behaviour (Botvinick & Braver, 2015), and a question of great scientific interest is if the decision to exert effort to achieve the desired outcome is able to elicit detectable changes in cognitive performance. In spite of the widely accepted belief that motivation enhances cognition, the relationship between these two distinctly treated constructs is not always that straightforward. The beneficial effect of reward on VWM performance is quite robust in younger adults, and can be tracked with less sensitive, all-or-nothing type of tasks as well. An intriguing question is however if the associations between motivational and cognitive functions are so unambiguous when either or both of these systems are corrupted, such as in psychiatric conditions, and also in healthy ageing. The number of studies investigating the effects of monetary incentives on various cognitive functions in older adults fall behind the literature examining younger groups, and their findings are far less consistent as well (Braver et al., 2014). Despite the central role of WM in goal-directed behaviour, and its sensitivity to the detrimental effect of healthy ageing, a single study investigated the modulatory effect of anticipated reward on the age-dependent changes in WM performance (Thurm et al., 2018). In line with the previous results on the motivation-cognition-ageing crossroad, this study provided mixed behavioural results as well. Crucially, the study of Thurm and colleagues employed an n-back task, conveying little information of the quality of WM representations therefore potentially masking more nuanced differences between the two age groups, that might be meaningful in terms of their reward sensitivity as well.

The aim of Study 4 (Manga et al., 2020) was to obtain detailed information on the motivation-cognition-ageing interaction in order to assess whether monetary incentives, and therefore, motivation might be a useful tool in counteracting the detrimental effects of healthy ageing on WM function. To assess the VWM performance, and the result of reward modulation, the study employed the previously introduced orientation delayed-estimation paradigm, allowing for the investigation of the resolution of VWM representations, just as the nature of the errors committed on the task (Gorgoraptis et al., 2011). The study involved a remarkably large sample of younger and older adults, who could collect points during the experiment as a function of the given trial's reward value (indicated at the beginning of each trial) and recall precision, converted to monetary reward at the end of the experiment. The results of Study 4 indicated that reward has a beneficial effect on the quality of VWM representations only in the group of younger adults, when recall precision – the overall measure of performance – was evaluated. In contrast, the analysis of the effect of anticipated monetary incentives on the decomposed errors committed on the task (Bays et al., 2009; Suchow et al., 2013) showed that the offered reward decreases the variability of the answers, the probability of misbinding of object features and the probability of guessing in younger and older adults as well. Importantly, the reaction times showed that older adults were motivated to give precise and elaborate responses just as younger adults, raising the intriguing possibility that age-related changes in the motivational guidance of behaviour manifest in the reduced capability to convert effort to improvement of overall WM performance. Taken together, these results add new and robust evidence to the literature, that the boosting effect of reward on WM is still present in old age, although undergoes a deterioration. Meanwhile, the present study also points out that the investigation of the motivation-cognition interaction requires sensitive methods like computational modelling for its characterisation. Moreover, these findings contribute to important avenues of therapeutic utilizations of motivation, exploiting its benefits in counteracting cognitive decline.

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