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REVIEW ARTICLE

Recent advancements in the investigation of visual working memory

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Abstract

Research of visual working memory has been dominated by efforts to establish the nature and origin of its apparent capacity limitation. Experiments focusing on visual working memory precision, rather than capacity, have yielded evidence for alternative models that operate with a shared continuous resource as opposed to a few discrete slots. Despite considerable research effort over the past two decades, the debate is still ongoing and new findings and hypotheses continue to emerge. We provide a short review of the most important findings with respect to visual working memory models, including the most recent proposals which try to unify the existing approaches into a common framework.

Introduction

Over the last two decades, visual working memory (VWM) has been a subject of intense research in the fields of cognitive psychology and neuroscience. WM enables performing complex tasks such as learning, perception, problem solving, or action control. It is considered crucial for a general cognitive ability and varies substantially across individuals (Baddeley 2003; Ma *et al.* 2014). One of the main open questions is the nature of VMW capacity limitation, which is restricted to 3–4 objects (Luck & Vogel 2013). Since Vogel and Machizawa (2004) established an electrophysiological index of this limit in storage capacity (the so-called *contralateral delay activity*, CDA), supporting the model of *discrete slots* (see below), numerous alternative models have been proposed to explain and integrate the new growing body of knowledge. These explain the apparent limit in capacity by a finite amount of resources which can be allocated between multiple objects with varying degrees of precision (*resource-based models*, e.g. Bays & Husain 2008; Ma *et al.* 2014), an interconnection between these two mechanisms, also referred to as *hybrid models* (Machizawa *et al.* 2020), or indeed an entirely new unifying framework, which is the alternative supported by the most recent evidence (Schneegans *et al.* 2020).

According to resource-based models, the limits VWM are best characterised by the *quality* or *precision* of memory, rather than the *quantity* of discrete items which are stored and subsequently recalled. These models are based on two basic premises: (a) the internal representations of sensory stimuli are corrupted by random fluctuations (noise), and (b) the level of such noise is proportional to the number of stored stimuli and attributed to limitations of the representational medium (whose precise nature remains to be established yet). The inherent presence of noise is in line with Bayesian models of perception, which postulate that observers make decisions based on noisy evidence using probabilistic inference, where performance increases continuously with signal-to-noise ratio. On the other hand, the increase in noise with set size is common to existing models of attention (Ma *et al.* 2014; Wilken & Ma 2004).

Ma *et al.* (2014) distinguished four classes of current VWM models:

a) *Discrete slots* – there is a number of independent memory slots where each item is stored with a high resolution. The items are then either recalled with high precision or guessed randomly depending on whether they received a slot.
b) *Equal resources* – there is a limited supply of some representational medium which is shared between all items without any limit on the number of items. The precision of recall depends on the amount of resource allocated to each item and since each item receives an equal share, the error variability increases with the number of items.
c) *Discrete representations* – the representational medium is divided into multiple slot-like quanta which are shared between items and may combine for low set sizes, thus increasing the resolution. For higher set sizes exceeding the number of available quanta, the model predicts a mixture of low-resolution recall and random guesses.
d) *Variable precision* – the precision varies between trials as well as individual items around a mean which decreases as the number of items increases.

In contrast to *discrete slots*, all other models (i.e. *equal resources*, *discrete representations*, and *variable precision*) can be classified as resource-based.

Evidence from behavioural studies

Wilken and Ma (2004) adapted and further developed the *delayed-estimation* technique based on changing the stimuli and response probes on a continuous scale (e.g. colour hue). This manipulates the signal-to-noise ratio in order to measure the level of noise in memory representations, as opposed to conventional discrete methods for probing working memory such as change detection or digit span where the stimulus or change in stimulus is held constant to produce a discrete measure such as the number of objects. The technique has been applied to a range of visual features such as colour (Fougnie *et al.* 2012; Wilken & Ma 2004), orientation (Gorgoraptis *et al.* 2011), or motion (Zokaei *et al.* 2011). For all features, recall variability (and hence imprecision) has been shown to gradually and continuously increase with set size, which is expected if resources are shared between multiple representations (Ma *et al.* 2014).

The flexibility in resource allocation is supported by a growing body of evidence indicating uneven distribution guided by voluntary control in order to increase the precision of prioritised items. For example, in studies where one stimulus in a memory array was marked as more likely to be selected as a later probe, a robust gain in recall was observed for the cued stimulus compared to other (non-cued) stimuli whose recall precision decreased (Bays *et al.* 2011a; Bays & Husain 2008; Gorgoraptis *et al.* 2011; Ma *et al.* 2014; Zokaei *et al.* 2011). Several facts indicate that these findings are not explained by biased sensory processing in favour of the prioritised items: (a) The results remain consistent when stimuli are presented sequentially one at a time, thus eliminating competition in sensory input. (b) Cues presented after a prolonged examination of a stimulus array as well as ones presented at the beginning of the stimulus interval are of similar effectiveness, suggesting that the resolution of working memory can change by a rapid reallocation after the initial encoding is complete to prioritise salient or goal-relevant information (Bays *et al.* 2011a). (c) Recall precision can be influenced by retrospective cues presented when the sensory input is no longer available (Ma *et al.* 2014; Pertzov *et al.* 2013a). Behavioural priorities thus seem to control the allocation of limited resources while similar recall advantages and costs have been shown for visually conspicuous objects even when the test probability was equal. This suggests a form of autonomous control which might be linked to visual attention, whose involvement was also supported by the observations of recall advantages for targets of saccades in humans and for targets of covert attentional shifts inferred from micro-saccades in rhesus monkeys (Bays *et al.* 2011a; Lara & Wallis 2012; Maurer *et al.* 2014; Melcher & Piazza 2011; Shao *et al.* 2010).

Another open question is the origin of the noise responsible for the variance in working memory precision. The errors in recollection of a stimulus could arise from multiple sources across all stages of information processing. This includes decreased precision of early sensory representations, for example due to physical stimulus properties such as luminance or contrast, or incomplete encoding of multiple or complex stimuli. This process is not instantaneous and when the time for encoding is systematically varied, the rate of recall precision increase depends on the number of visual elements (Bays *et al.* 2011a). Another potential sources are the attentional or storage capacity limitations, manifested by a limit on the precision even over prolonged exposure. This is in line with the experimental evidence introduced with discrete models (Ma *et al.* 2014). The errors could also emerge during maintenance, as evidenced by the increase in recall variability proportional to the duration of the delay period (Pertzov *et al.* 2013b).

Contributions from neuroscience

The RThe majority of computational VWM models assume that the retention of visual representations occurs in a recurrent feedback loop between multiple neuronal populations, which explains an increase in neural activity during the retention period. According to models based on recurrent neural networks, object representations are formed and maintained by dynamically-formed synchronous neuronal populations, while asynchronous activity of such units allows multiple representations to co-exist (Deco & Rolls 2008; Luck & Vogel 2013). Using biologically realistic parameters, these models reveal capacity limitations similar to *in vivo* findings (Raffone & Wolters 2001). The number of oscillatory states that can be superimposed without interference could thus explain the capacity limitations within the framework of slot-based models, however physiological evidence for oscillatory models has been sparse (Lisman & Idiart 1995; Ma *et al.* 2014).

On the other hand, rate coding of WM representations seems to be compatible with resource-based models. During WM encoding, the number of action potentials varies considerably from trial to trial, which might be the source of noise present during recall (van den Berg *et al.* 2012; Ma *et al.* 2014; Ma & Huang 2009). Furthermore, an interconnection between the memory resource and the magnitude of neural activity (gain) in a neural population representing an object is supported by a body of evidence. For example, models of early sensory representation postulate that the neural gain is proportional to the stimulus encoding precision (Ma *et al.* 2006) and note the presence of similarities between resource for working memory and attention, where the latter has been shown to modulate neural gain (Awh & Jonides 2001; Mazyar *et al.* 2012; McAdams & Maunsell 1999). Furthermore, neurophysiological evidence shows that firing rate is inversely proportional to increasing set size (Churchland *et al.* 2008) and varies between trials (Churchland *et al.* 2011), or that energy conservation leads to fewer spikes at the cost of decreased precision at large set sizes (van den Berg *et al.* 2012; Ma *et al.* 2014). Computational models involving shared resource mechanisms support the plausibility of the resource-based accounts of WM, yielding decreased memory precision with increasing set size, in agreement with behavioural findings (Wei *et al.* 2012).

Functional neuroimaging studies have identified regions within prefrontal and posterior parietal cortex with elevated activity during working memory maintenance (Linden *et al.* 2003; Todd & Marois 2004) while electroencephalographic (EEG) studies observed for example the already mentioned CDA (Anderson *et al.* 2011; Vogel & Machizawa 2004), both reflecting the number of items in memory (Ma *et al.* 2014). Neural activity increases with memory load for up to 3–4 objects, but reaches plateau at higher loads. This has been interpreted as reflecting the maximum WM capacity and thus a property predicted by slot-based models. However, establishing the significance of a signal plateau in the presence of noise is not trivial and the methods used so far have relied either on subjective visual judgement or statistical testing. It is therefore necessary to establish whether the signals reach a maximum when a particular number of objects is presented, or further increase with increasing number of objects toward an asymptotic limit (Ma *et al.* 2014). Furthermore, the basis for the neural correlates of WM performance might be more complex than assumed. For instance, it has been suggested that the increase in CDA amplitude may result from averaging of EEG oscillations in the alpha band (9-13 Hz) whose power is modulated asynchronously over multiple trials (van Dijk *et al.* 2010). Resource-based models, on the other hand, postulate utilisation of the same resources regardless of the number of objects that are being stored, yet load-dependent signals can still be explained in terms of reflecting increased synaptic processing as a result of increasing set size. They might also be associated with the maintenance of "meta-information" facilitating resource allocation or bindings between different features (Bays *et al.* 2011b; Ma *et al.* 2014; Wheeler & Treisman 2002).

The ongoing debate

Adam *et al.* (2017) brought yet more evidence for item limits in VWM. They developed a new experimental paradigm in which participants recalled the precise colour or orientation of every displayed item irrespective of the order and assumed that if there are no item limits, some amount of information should be measurable across all responses. They found that participants consistently reported items in the decreasing order of precision and that the final three responses were best modelled by a parameter-free uniform distribution, indicating guessing. In order to explore a key claim of the variable precision model – that all representations contain measurable information – they also used computational simulations and showed that there is little evidence to reject guessing in favour of memories that contain extremely little information and thus become indistinguishable. These results thus support a model of a discrete capacity limit, which is often not achieved likely due to fluctuations in attentional control (Adam *et al.* 2015, 2017).

Bays (2018) subsequently addressed these conclusions by pointing out that rather than demonstrating change in performance indicative of individual capacity being reached, Adam and co-workers arbitrarily set the level of variability beyond which responses were considered uniform (and thus pure guesses). He further argued that the results can be well explained also by resource models with no fixed capacity and showed that estimations of individual capacity can yield inconsistent results when the slot-based model is adopted.

Most recently, Schneegans *et al.* (2020) used a novel approach rooted in the principles of neural coding as a framework for explaining VWM limits and demonstrated that three of the most prominent competing models can be expressed in terms of the same unifying mathematical framework of sampling. The sampling interpretation of VWM models proposes that coding performed by a neural population should be reinterpreted as sampling, i.e. the evoked response of an idealised population of spiking neurons to a stimulus depends on their individual tuning described by the tuning function and the preferred value. Associating spikes over a fixed decoding window with the preferred stimuli of the respective neurons creates a probability distribution over stimulus space that is then used to create a maximum likelihood estimate, assuming the same total activity when encoding multiple items, where larger set sizes correspond to less mean activity per item. Precision is defined as the width of the likelihood function and discretely distributed as a product of tuning precision and the number of spikes, which varies stochastically. The retrieval of a visual feature from VWM can then be described as estimation based on stochastically varying number of noisy samples. According to the authors, two other influential models of VWM can be reconceptualised using the same framework: (a) *the discrete representations model* (referred to by the authors as slots+averaging), which is directly equivalent to a sampling model with a fixed number of samples; (b) *the variable precision model*, where samples become less precise and more numerous, while maintaining fixed proportionality between variance and mean of the precision in the decoded estimate. This allowed Schneegans and co-workers to identify the key differences between the models as well as the critical factors to account for the differences in experimental data that do not decisively favour either one of the main 'standard' models. Importantly, this new approach is agnostic with regard to whether objects or features are the units of VWM storage, because both options are compatible and depend on whether the encoding neurons are sensitive to sole features or their conjunctions.

Conclusion

Despite the apparent shift towards understanding the nature of the capacity limitation of VWM as a continuous resource guided by attentional selection, the debate and competition between various models is ongoing. The most recent re-conceptualisation by Schneegans *et al.* (2020) offers an intriguing novel framework with a unifying potential that provides new opportunities for further research. The sampling framework certainly has some limitations, which are yet to be explored in detail, but the approach has been gaining popularity in neuroscience as a neurobiologically plausible account of how Bayesian inference may be performed online in the brain as it is presented with new information (Radulescu *et al.* 2021). For VWM, the current knowledge thus seems to favour resource-based approaches that implement the characteristics which result in some sort of discretisation.

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REFERENCES

1 Adam KCS, Mance I, Fukuda K, Vogel EK (2015). The contribution of attentional lapses to individual differences in visual working memory capacity. *J Cogn Neurosci.* **27**(8): 1601–1616.
2 Adam KCS, Vogel EK, Awh E (2017). Clear evidence for item limits in visual working memory. *Cogn Psychol.* **97**: 79–97.
3 Anderson DE, Vogel EK, Awh E (2011). Precision in visual working memory reaches a stable plateau when individual item limits are exceeded. *J Neurosci.* **31**(3): 1128–1138.
4 Awh E & Jonides J (2001). Overlapping mechanisms of attention and spatial working memory. *Trends Cogn Sci.* **5**(3): 119–126.
5 Baddeley A (2003). Working memory: Looking back and looking forward. *Nat Rev Neurosci.* **4**(10): 829–839.
6 Bays PM, Gorgoraptis N, Wee N, Marshall L, Husain M (2011a). Temporal dynamics of encoding, storage, and reallocation of visual working memory. *J Vis.* **11**(10): 6–6.
7 Bays PM & Husain M (2008). Dynamic shifts of limited working memory resources in human vision. *Science.* **321**(5890): 851–854.
8 Bays PM (2018). Failure of self-consistency in the discrete resource model of visual working memory. *Cogn Psychol.* **105**: 1–8.
9 Bays PM, Wu EY, Husain M (2011b). Storage and binding of object features in visual working memory. *Neuropsychologia.* **49**(6): 1622–1631.
10 Churchland AK, Kiani R, Shadlen MN (2008). Decision-making with multiple alternatives. *Nat Neurosci.* **11**(6): 693–702.
11 Churchland AK, Kiani R, Chaudhuri R, Wang XJ, Pouget A, Shadlen MN (2011). Variance as a signature of neural computations during decision making. *Neuron.* **69**(4): 818–831.
12 Deco G & Rolls ET (2008). Neural Mechanisms of Visual Memory: A Neurocomputational Perspective. In: Luck SJ & Hollingworth A, editors. Visual Memory. Oxford University Press, pp. 247–290
13 Fougnie D, Suchow JW, Alvarez GA (2012). Variability in the quality of visual working memory. *Nat Commun.* **3**(1): 1229.
14 Gorgoraptis N, Catalao RFG, Bays PM, Husain M (2011). Dynamic updating of working memory resources for visual objects. *J Neurosci.* **31**(23): 8502–8511.
15 Lara AH & Wallis JD (2012). Capacity and precision in an animal model of visual short-term memory. *J Vis.* **12**(3): 13.
16 Linden DEJ, Bittner RA, Muckli L, Waltz JA, Kriegeskorte N, Goebel R, et al. (2003). Cortical capacity constraints for visual working memory: Dissociation of fMRI load effects in a fronto-parietal network. *Neuroimage.* **20**(3): 1518–1530.
17 Lisman JE & Idiart MAP (1995). Storage of 7 ± 2 short-term memories in oscillatory subcycles. *Science.* **267**(5203): 1512–1515.
18 Luck SJ & Vogel EK (2013). Visual working memory capacity: From psychophysics and neurobiology to individual differences. *Trends Cogn Sci.* **17**(8): 391–400.

19 Ma WJ, Beck JM, Latham PE, Pouget A (2006). Bayesian inference with probabilistic population codes. *Nat Neurosci.* **9**(11): 1432–1438.
20 Ma WJ & Huang W (2009). No capacity limit in attentional tracking: evidence for probabilistic inference under a resource constraint. *J Vis.* **9**(11): 3.1–30.
21 Ma WJ, Husain M, Bays PM (2014). Changing concepts of working memory. *Nat Neurosci.* **17**(3): 347–356.
22 Machizawa MG, Driver J, Watanabe T (2020). Gray matter volume in different cortical structures dissociably relates to individual differences in capacity and precision of visual working memory. *Cereb Cortex.* **30**(9): 4759–4770.
23 Maurer U, Brem S, Liechti M, Maurizio S, Michels L, Brandeis D (2014). Frontal midline theta reflects individual task performance in a working memory task. *Brain Topogr.* **28**(1): 127–134.
24 Mazyar H, van den Berg R, Ma WJ (2012). Does precision decrease with set size? *J Vis.* **12**(6): 10.
25 McAdams CJ & Maunsell JH (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *J Neurosci.* **19**(1): 431–441.
26 Melcher D & Piazza M (2011). The role of attentional priority and saliency in determining capacity limits in enumeration and visual working memory. *PLoS One.* **6**(12): e29296.
27 Pertzov Y, Bays PM, Joseph S, Husain M (2013a). Rapid forgetting prevented by retrospective attention cues. *J Exp Psychol Hum Percept Perform.* **39**(5): 1224–1231.
28 Pertzov Y, Miller TD, Gorgoraptis N, Caine D, Schott JM, Butler C, Husain M (2013b). Binding deficits in memory following medial temporal lobe damage in patients with voltage-gated potassium channel complex antibody-associated limbic encephalitis. *Brain.* **136**(8): 2474–2485.
29 Radulescu A, Shin YS, Niv Y (2021). Human representation learning. *Annu Rev Neurosci.* **44**(1): 253–273.
30 Raffone A & Wolters G (2001). A cortical mechanism for binding in visual working memory. *J Cogn Neurosci.* **13**(6): 766–785.
31 Schneegans S, Taylor R, Bays PM (2020). Stochastic sampling provides a unifying account of visual working memory limits. *Proc Natl Acad Sci.* **117**(34): 20959–20968.
32 Shao N, Li J, Shui R, Zheng X, Lu J, Shen M (2010). Saccades elicit obligatory allocation of visual working memory. *Mem Cogn.* **38**(5): 629–640.
33 Todd JJ & Marois R (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature.* **428**(6984): 751–754.
34 van den Berg R, Shin H, Chou W-C, George R, Ma WJ (2012). Variability in encoding precision accounts for visual short-term memory limitations. *Proc Natl Acad Sci.* **109**(22): 8780–8785.
35 van Dijk H, van der Werf J, Mazaheri A, Medendorp WP, Jensen O (2010). Modulations in oscillatory activity with amplitude asymmetry can produce cognitively relevant event-related responses. *Proc Natl Acad Sci.* **107**(2): 900–905.
36 Vogel EK & Machizawa MG (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature.* **428**(6984): 748–751.
37 Wei Z, Wang X-J, Wang D-H (2012). From distributed resources to limited slots in multiple-item working memory: a spiking network model with normalization. *J Neurosci.* **32**(33): 11228–11240.
38 Wheeler ME & Treisman AM (2002). Binding in short-term visual memory. *J Exp Psychol Gen.* **131**(1): 48–64.
39 Wilken P & Ma WJ (2004). A detection theory account of change detection. *J Vis.* **4**(12): 11.
40 Zokaei N, Gorgoraptis N, Bahrami B, Bays PM, Husain M (2011). Precision of working memory for visual motion sequences and transparent motion surfaces. *J Vis.* **11**(14): 2.