When and Why Does Visual Working Memory Capacity Depend on the Number of Visual Features Stored: An Explanation in Terms of an Oscillatory Model

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Abstract

The nature of capacity limits within human visual working memory (VWM) remains the subject of controversy: while the capacity-as-objects account predicts that what loads VWM capacity is solely the number of objects maintained, irrespectively of the number of visual features that need to be stored for each object, the capacity-as-features account predicts that also (or - primarily) the total number of features maintained in VWM loads its capacity (and leads to decreased performance). We present novel simulations of a VWM task, using our existing, oscillatory computational model that describes the binding of features into objects as resulting from the proper synchronization and desynchronization of rhythmical changes in neuronal activity. The model predicted (in line with wide evidence) that VWM performance decreases with the increasing number of objects, but also decreases (although not as sharply as predicted by the capacity-as-features account) as a function of increasing number of features. The model attempts to explain what precise characteristics of oscillatory dynamics stand behind such two sources of VWM limitation. However, the complete pattern of the model's predictions remains yet to be examined empirically.

Introduction

Working memory (WM) is a neurocognitive mechanism responsible for the active maintenance of information as well as its manipulation for the purpose of the current task. Although early research on WM was dominated by verbal paradigms and models, for the last 15 years some researchers (e.g., Luck & Vogel, 1997) have pointed at the crucial role of, relatively simpler than verbal WM, visual working memory (VWM; also called robust visual shortterm memory store) in subserving functions of temporary storage, binding, and manipulation of information. VWM operates on visuospatial representations, usually called objects, that are widely thought to consist of bindings of the corresponding visuospatial features (like shape, color, orientation, size, or location). Although simple, during the evolution of the human mind this mechanism, primarily responsible for the continuity of perception as well as the spatial orientation, most probably has been adapted in service of more complex cognition, including the construction of abstract representations (see Cowan et al., 2011), encoding and processing relations (Clevenger & Hummel, 2014), as well as running mental models and simulations (hypothetical models of the world, in abstraction from its actual state; Johnson-Laird, 2006). This hypothesis is supported by the fact that WM (and VWM in particular) is the strongest known predictor of fluid intelligence - the crucial ability to solve new, complex problems, that is central to human cognitive ability (McGrew, 2009). It has been shown that VWM capacity, measured by the number of recalled or recognized visual representations, explains up to half of variance in fluid intelligence (Fukuda, Vogel, Mayr, Awh, 2010), what suggests a key role of VWM in reasoning, but also in other types of complex cognitive processing, like problem solving, spatial navigation, language use, complex learning, and decision making (i.e., those strongly correlated with fluid intelligence).

Research on VWM pertained to such issues as the role of attentional selection/filtering in VWM, the profound influence of global organization of perceptual scene (statistical regularity) on the number of objects that can be retrieved from VWM, as well as the interaction of VWM and long-term memory (for a review see Brady, Konkle, & Alvarez, 2011). Also, a lot is known about neurobiological basis of VWM, including localization of VWM subsystems responsible for maintaining object features (within superior parietal lobule) versus binding complete objects out of those features (within inferior parietal lobule; Xu & Chun, 2009), or the relation between individual capacity observed in people and the patterns of activity of these subsystems (Todd & Marois, 2004).

Indeed, one of the most important features of VWM is that its capacity is heavily limited and inter-individually varied. Usually, the average capacity of VWM equals four objects or even less, and in the population it can vary from two up to six items (Cowan, 2001). However, the major controversy in research on VWM capacity is what exactly is its "currency", that is, which aspect of maintained information limits the number of objects stored and retrieved. Early theories proposed that VWM is limited in its capacity for storing separate objects, irrespectively of the complexity of particular objects (Luck & Vogel, 1997; for a review see Fukuda, Awh, & Vogel, 2010). The evidence for this stance came from studies in which increasing the number of presented objects drastically decreased performance (usually measured with the so-called change detection paradigm that requires remembering one visual array, as well as its later comparison with either the identical array or an array in which one item has been changed; Cowan, 2001; Luck & Vogel, 1997). At the same time, performance seemed to be robust to increasing number of visual features that had to be encoded and processed (e.g., people detected the change for several simple objects, like squares, that differed only in color with a comparable accuracy as they detected the multiple-feature objects).

However, recently many scholars (e.g., Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; for a review see Brady, Konkle, & Alvarez, 2011) have objected this capacity-as-objects account, suggesting that in fact what constrains VWM is the total amount of information in a perceptual scene, and people remember a larger number of perceptually simpler objects than of complex, multiplefeature objects (Alvarez & Cavanagh, 2004). According to the capacity-as-features account, the changes imposed in the change detection paradigm are too substantial (e.g., a change from red to blue) in order to reveal the influence of VWM load on the precision of maintained representations, which however does appear when participants are asked to reproduce exact values of remembered visual features (i.e., "was it light red, dark red, or pink?"). The methodological and interpretational issues concerning new paradigms for VWM capacity measurement remain controversial (for opposing views see Brady et al., 2011, and Fukuda et al., 2010). However, a recent study (Oberauer & Eichenberger, 2013) has shown that even in the standard change detection paradigm (but probably under better experimental control than in previous studies), the VWM performance gradually dropped when three objects were presented with one, three, or as much as four or six visual features (picked up from the following features: color, shape, orientation, size, the thickness of bars inside, and the frequency of stripes inside.

Also other accounts exist, for example a recent view (Clevenger & Hummel, 2014) which suggested that the "objects" of VWM are neither complete objects or feature-object bindings, but the pairs of objects. According to this *capacity-as-paired-relations* account, the capacity of VWM is constrained by the number of representations of pairs of objects, bound with all spatial relations between these objects, and encoded in parallel.

Apart from behavioral experimentation, another way to understand the nature of VWM is to develop (and test) process models of VWM that show in simulations which stages or characteristics of visual information processing are the most vulnerable to WM load, and why VWM capacity has to be limited (because of certain processing demands). The most influential line of such models consists of *oscillatory models* (e.g., Horn & Usher, 1992; Raffone & Wolters, 2001; Usher, Cohen, Haarmann, & Horn, 2001; Vogel, Woodman, & Luck, 2001) that describe the binding of features into objects as resulting from the proper synchronization and desynchronization of rhythmical changes in neuronal activity, called *brain oscillations*. Binding of features into an object is made with synchronous oscillations, whereas the maintenance of separable objects – with asynchronous oscillations. Features of the same item fire in synchrony, whereas two features of different objects are active out of phase. Due to this mechanism, the system is able to reconstruct the object from its features. Such an oscillatory nature of VWM has recently been demonstrated in both primates (e.g., Siegel, Ward, & Miller, 2009) and humans (Kaminski, Brzezicka, & Wrobel, 2011).

The goal of the present study is to analyze how the modified version of one such model of VWM, originally proposed by Chuderski, Andrelczyk, and Smolen (2013), handles different numbers of objects and features in its memory, and to identify what characteristics of a dynamic, oscillatory system implemented in the model may be responsible for its limited capacity to store either objects or features, or some product of objects and features. We start with a concise description of the above mentioned model.

An oscillatory computational model of visual working memory

The main part of the model consists of a buffer, which contains a certain number of elements. Each element roughly approximates a neuronal assembly representing one specific feature of the world. Like in many other models (e.g., Horn & Usher, 1992; Raffone & Wolters, 2001), a level of internal activation x_i is assigned to each element *i*. The following equation defines the change in the level of activation *x* of *i*th element from time *t* to time *t*+1:

$$x_{it+1} = x_{it} + \frac{\omega}{1 + \frac{1}{e^{-x_{it}^{-0.5}}}} + \alpha \sum_{|x_{jt} - x_{it}| \le \delta} e^{x_{jt} - x_{it}}$$
$$-\beta \sum_{|x_{kt} - x_{it}| > \delta} e^{x_{kt} - x_{it}} + \varepsilon(n)$$

This equation consists of five components. The first component is simply the activity of element *i* in the preceding cycle. The second component represents the self-recurrent increase of the activation of element *i*, reflecting the reverberatory nature of neuronal assemblies constituting WM. The output of *i* is fed back to *i* in order to increase *i*'s activity. The parameter ω impacts the frequency of oscillations given a particular time scale, but has no significant influence on the model's capacity. The output of the element *i* in time *t* has been defined using a commonly applied sigmoid function of x_i .

The third component of the formula represents the *coactivation* of *i* by the mean activity of elements *j* that fire in close proximity with *i*, that is, whose activity x_j falls within $[x_i - \delta, x_i + \delta]$. Such a range denotes the activity horizon in which all oscillating elements are treated as

forming one *binding* that integrates features into a particular object, an object with its context, or a role-argument pair. This component accounts for the known fact that neurons that all fire in synchrony with a given neuron more strongly influence its potential as well as synaptic connections than when they fire out of phase. The less active element *j* is, the less it can coactivate *i*. Moderate values of δ have no negative influence on the model's capacity, unless δ is either too small ($\delta < 0.01$) or too large ($\delta > 0.1$), that is, when the bound elements are either highly prone to random changes in activation (i.e., they easily fall apart) or there is no place in the activity space to add new distinct items (i.e., $x_i + \delta$ approaches x of another, more activated item), respectively. Parameter α regulates the amount of coactivation that is spread from *j* to *i*. Initial computational simulations showed that it has a limited influence on the model's capacity, as its low value ($\alpha = 0.0004$) used in the present simulation yielded quite similar capacity (5.1 two-element items) as (5.5 items) its optimal value ($\alpha = 0.0012$; no further gains in capacity were noted).

The fourth component implements the most important mechanism of the model: lateral inhibition exerted by the bindings that are treated as encoding distinct representations from a representation encoded by elements *i* and *j*; that is, the elements denoted by *k*, which fall outside the range $[x_i - \delta, x_i + \delta]$. The less active element *k* is, the less it inhibits *i*. The larger the activation of an inhibiting binding, the more it suppresses element *i*. Parameter β controls the strength of that inhibition. Previous simulations (see Chuderski et al., 2013) demonstrated that β is the main factor controlling the capacity of our oscillatory model. An increase in β negatively impacted available capacity, as higher values of β made more elements to fall out from VWM (drop permanently below the threshold arbitrarily set to .2).

The last component consists of the noise ε , drawn from the normal distribution with the mean equal to zero, and the variance dependent on the parameter *n*. Large noise (*n*>0.00005) negatively influences capacity, as oscillations of elements become more random; however, its small values (*n*<0.00001) affect the capacity only slightly.

When the output of element *i* surpasses unity (this reflects the strongest possible firing of a neuronal group), the parameter ω for that element is temporarily reversed (reflecting the well-known phenomenon of neuronal hyperpolarization), causing this element to fall quickly below the threshold of activation (0.2), what represents the mechanism of refraction (afterhyperpolarization). When x_i becomes smaller than the threshold, ω value is reset to a previous positive value, and the element starts building up its activation above the base level. However, in certain cases the inhibition signals may be so strong that the activation of *i* is too slow, and just after ω is reversed the activation of *i* decreases permanently below the threshold - the minimal activation necessary to stay in WM. If this happens, element *i* falls out of WM, meaning that it can no longer impact other elements in WM, nor can be recalled (but it may potentially be encoded in the active part of long-term memory). This latter mechanism underlies the function of emptying WM in order to encode incoming information.

Generally, the number of elements which can be bound together within one synchronic oscillation is not limited. However, in Chuderski et al. (2013) only pairs of synchronized elements (an object identity and one its feature) were added to the model's VWM. So, how the model works when an object is composed from more visual features?

Workings of the oscillatory model

The aim of the model is to maintain as many separate oscillations as necessary, for a given time interval. Two elements making one oscillating pair (e.g., an object and the information about its a shape) are added to the buffer in the same time. The pair which is added as the first one is added with a random level of activation. Subsequent pairs can be added when activation of all other pairs is less than the value of $1 - 4 \times \delta$, and those subsequent pairs are added at a level of $x = x_{max} + \delta + (1 - x_{max}) / 2$, where x_{max} denotes the *x* value of the most active pair. So, this mechanism checks if there is enough place in the activation space for new elements, and grants that at least on entering the buffer the new pairs will be sufficiently distinctive from all pairs already maintained.



Fig.1: The model dynamics under increased VWM load.

In the model, the capacity limit arises because when the total amount of inhibition in the model is very large, it overcomes the results of activation, and the elements with the lowest activation levels start falling out of the buffer. If one element from the pair falls out, then the coactivation is no longer possible, and the chance that the other element from that pair would also fall out drastically increases. However, a certain amount of inhibition is necessary, because it secures that oscillations will evenly occupy a respective time interval, helping to separate them. So, the values of β reflect the trade-off between low inhibition (many objects can be maintained, but their bindings more easily fall apart) and high inhibition (less objects can be maintained, but their bindings are more robust).

Simulating the effects of objects and features' load on visual working memory capacity

Below, we report simulations in which, apart from the number of objects presented to our oscillatory model in the (simulated) change detection task, we varied the number of features per object. When the arrays in the task changed, than a random number of features were altered in the highlighted target (i.e., from one feature to the maximum number of features possible). Thus, the model had to maintain in its VWM all features of an object, because if it encoded only some features, and the changed feature was among remaining ones (was not encoded), the model would commit an error of omission. We compared the results of our simulations to existing empirical data. The classic study (Vogel et al., 2001; Experiments 11 & 14) yielded a large effect on the change detection accuracy of the number of objects that were required to maintain (either 2 or 4 objects), but no effect of the number of features per object (1 or 4). In contrast, Oberauer and Eichenberger (2013) used eight feature values per each featural dimension, and observed a significant drop in participants' performance when the number of featural dimension increased from one to four. So, can our oscillatory model replicate this data (see Fig.3)?

We simulated the variant of the change detection task similar to the variant applied by Oberauer and Eichenberger, as their results seem to be the most reliable data available. However, unlike their use of only sets of three objects, we manipulated the number of presented objects at three levels: two, three, and four, in order to observe whether any interaction of the numbers of objects and features occurs. First, the model was presented with symbolic descriptions (no perceptual module was modeled) of objects that contained the numerical identity of an object (e.g., Object1) plus one, two, or four values of distinct features. The task of the model was to encode the objects in its oscillatory VWM, and to maintain these objects until the description of the second array arrived. This array could be identical (in half trials) or could differ in a random number of features for exactly one object indicated (in the remaining half of trials). Finally, the model decided if the target object matched the corresponding contents of VWM, or differed. The accuracy of the model's responses was recorded.

In the following simulations, we used exactly the values of parameters fitted to data in the previous simulation (Chuderski et al., 2013). That is, we set parameter α to a value of .0004, parameter ω was drawn from the normal distribution with $\mu = 0.05$, and $\sigma = 0.005$, and parameter δ was set to $\delta = .05$. The only parameter we analyzed, and fitted in the present study, was the value of β (in the original paper the mean value of $\beta = .0026$ was used).

Simulation results

First, we analyzed how parameter β determines the overall accuracy in the current version of the model. We simulated 450 trials in the change detection task per each reasonable value of β (.0010, .0015, .0020, .0025, and .0030), using only the set sizes of three objects, as well as applying the number of features equaling one, two, or four (i.e., the exact values used by Oberauer & Eichenberger in their Exp. 3). The results, shown in Fig. 2, indicated that a moderate level of β between .0015 and .0020 was optimal. At either higher or lower values of β accuracy dropped substantially. The probable cause of the fact that too low inhibition deteriorated VWM maintenance results from stochastic effects that pertain to the activations of oscillated elements. When the model tried to maintain many bindings, low inhibition was not able to optimally separate the consecutive oscillations, the activations within one binding (object) might vary more than was the distance (in the activation space) to subsequent bindings, and some elements might fall into the attractor of another binding. Obviously, a high level of inhibition was not effective either: bindings mutually inhibited themselves so strongly that elements that entered the afterhyperpolarization phase were easily eliminated from the model.

Thus, in the following simulations we adopted the optimal levels of β , picking it up on random from [.0014 – .0021] range. The simulation contained set sizes of two, three, and four objects, which could be the bindings of two elements (an object's numerical identity + the value of one its feature), three elements (an object + two features), and five ones (an object + four features). Thus, for each set size we calculated three data points (i.e., nine data points were obtained with fitting only one parameter). In total, 1800 trials were simulated per each data point.



Fig. 2. The average accuracy of the model in the threeobject change detection task under varying levels of β .

Not surprisingly, the model replicated the effect of the number of to-be-remembered objects on accuracy, overall matching the usual pattern of empirical data. Regarding the number of features, the results of set size equaling three nicely matched data of Oberauer and Eichenberger (2013): the model aptly mimicked the fact that accuracy decreased when the number of features increased, F = 92.02, p < .001, however the simulated decrease (19%) was slightly larger than the one observed by Oberauer and Eichenberger (10%).



Fig. 3. Upper panel: data from Vogel et al. (2001) for set sizes two and four, and from Oberauer and Eichenberger (2013) for set size three. Bottom panel: data simulated by the oscillatory model (black line = mean from all set sizes). Bars = 95% confidence intervals.

For set sizes two and four, we could compare simulated data with the results of Vogel et al., who used exactly such set sizes. For set size four, our data diverged from their results, because there was a similar drop in accuracy as a function of the number of features, F = 6.57, p = .001, as was in the three-objects condition. The same occurred when only two objects were presented to the model, F = 39.26, p < .001. The simulated data as well as data of Vogel et al., and Oberauer and Eichenberger, are presented in Fig. 3. What is apparent in Vogel et al., data is the huge ceiling effect, and

only marginal drop in accuracy from set size two to four. In consequence, the null effect of the number of features in Vogel et al. for some unknown reason might have resulted from their ceiling effect. In contrast, simulated data more closely matched Oberauer and Eichenberger data, who observed much lower accuracy for set size three than did Vogel et al. for set size four (and even than their set size six). Thus, the prediction of Oberauer and Eichenberger that the number of features maintained loads on WM and affects accuracy, congruent with our simulation results, seems to be more realistic.

In the model, both the number of objects and features affected accuracy because increasing each number increased the total amount of lateral inhibition. However, the impact of additional objects was stronger than the impact of features (i.e., it was easier to maintain two two-feature objects than four one-feature objects). The likely cause of such an effect consists of the fact that increasing the number of features increased both inhibition (decreasing overall capacity) and – to some extent – coactivation (increasing capacity). Thus, the negative effect of additional features was partially attenuated by more robust representation of each object. Increasing the number of objects increased only inhibition, but not coactivation, so it impact was stronger.

Discussion

Using a novel oscillatory model, which aimed to describe the functioning of human VWM, in line with the capacityas-objects account we showed that the major limitation of VWM in our simulations resulted from the number of to-bemaintained objects. However, we also demonstrated that, apart from the number of objects, also the number of visual features maintained in VWM may be limited. When the number of features became increased (especially, to four features), the system, being close to the maximum overall amount of lateral inhibition it could handle, could not maintain additional features with the same accuracy as one feature. This mechanism seems to explain well the data obtained within the capacity-as-features account (Oberauer & Eichenberger, 2013; Cowan et al., 2013).

Although the present model is limited by both the number of objects and the number of features it can effectively maintain, the model does not support the explanations of VWM capacity in terms of the total informational resource that is consumed by both the objects and the features (Bays, Catalao, & Husain, 2009; Bays & Husain, 2008). First, although the drop in accuracy did result from additional features, the performance of the model decreased much more slowly than did increase the total number of features. For example, accuracy for four features stored in the fourobjects-one-feature condition was only 10% higher than accuracy in the four-objects-four-features condition, even though the total number of features maintained increased from 4 to 16 features. This is not in line with predictions of the sheer limited-resource account. Additional assumptions made to this approach that would explain that the more features, the less VWM resource on average is consumed by a feature, help only a little. As cogently noted by Oberauer and Eichenberger (2013), such add-ons supplementing the limited-resource account made it virtually unfalsifable.

However, even though the present model is more compatible with those accounts of capacity that postulate that its currency are available slots in VWM (one slot = one object), but with more features per object the probability that surplus features will not be encoded effectively, it seems to nicely extend these accounts. Most of existing slot models were formulated as pure mathematical formulae that yield the probability of the correct change detection as a function of the number of objects, the number of features, and sometimes some additional parameters (e.g., Cowan et al., 2013; Oberauer & Eichenberger, 2013). In contrast, the present model is a process (i.e., computational) model that not only describes the relation between the characteristics of the change detection task and the resulting detection accuracy, but also generates the very complex dynamics (interpreted at the neural level) underlying the performance on this task. For example, the model explains the nature of slots in terms of dynamic bindings that interact mutually, and are prone to stochastic as well as chaotic effects.

To conclude, the presented dynamic model of VWM provided the prediction that although the VWM capacity is strongly constrained by the number of maintained objects (which is a widely observed fact), it is also, though more weakly, limited by the number of features per object (the factor that so far has not been examined exhaustively, and still awaits the comprehensive empirical study). In general, the study implies that in cognitive science at least for some research problems more can be theoretically understood from the development of process models, generating a particular phenomenon, than from pure mathematical models that only describe such phenomenon.

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