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An oscillatory model of individual differences in working memory capacity and relational integration ☆

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Abstract

We present a novel computational model of the active buffer of working memory (WM). The model uses synchronous oscillations in order to bind an item and its corresponding context into one representation, while asynchronous oscillations are used to separate the representations. Due to the bindings, the model can ascribe proper meanings to items, as demonstrated by the replication of the effective rejection of distractors. The model predicts the inherent limitation of WM capacity in range of 1 to around six items that arises from the trade-off between the number and stability of separate oscillations. This trade-off depends on the strength of lateral inhibition exerted. The systematic variation in inhibition led to the exact replication of capacity distribution observed in a large sample, as well as to the prediction of a few novel capacity-related experimental effects. Finally, we showed that the differences in capacity can underlie the differences in a more complex ability of detecting relations governing a pattern of stimuli, called relational integration, which is known to be strongly related to the effectiveness of higher-order cognitive processing.

Keywords: Working memory; Relational integration; Reasoning; Computational modeling

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1. Introduction

Working memory (WM) is a neurocognitive mechanism responsible for the active maintenance of information for the purpose of its ongoing processing during cognitive tasks. One of the most important features of WM is its heavily limited capacity. Usually, the average capacity of WM equals four objects (items), irrespectively of their complexity (Fukuda, Awh, & Vogel, 2010; Luck & Vogel, 1997; but see Brady, Konkle, & Alvarez, 2011). However, the substantial individual differences in WM capacity can be observed, as in the population it can vary from two up to six items (Cowan, 2001). Individual WM capacity plays a crucial role for performance in many complex cognitive processes, like learning, language, relational reasoning, and problem solving (Jarrold & Towse, 2006).

Influential theories of working memory structure (Cowan, 2001; Oberauer, Süß, Wilhelm, & Wittman, 2008; O'Reilly, 2006) predict that WM consists of two distinct systems: a highly active and accessible buffer called *the focus of attention* (or, *primary memory*; PM), and a less accessible *activated long-term memory* (or, *secondary memory*; SM). It is argued that PM allows for active maintenance of and direct access to information, but its capacity is heavily limited, while access to items stored in SM is less direct, but SM capacity is not limited in the same way. Thus, it is PM that primarily influences human performance on various intellectual tasks (Cowan, 2001).

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The brain locus of the active buffer was identified as the inferior intraparietal sulcus, and it was shown that indeed its activation plateaus at a load of a few items (Todd & Marois, 2004).

The most promising theoretical approach to information storage in PM explains it as a kind of oscillatory pattern. Several neurally plausible models of PM describe the mechanisms which use patterns of fast, repetitive changes in the activity of stored representations (i.e., use more than one oscillation during a retention time) for coding items in PM (Edin et al., 2009; Horn & Usher, 1992; Jensen & Lisman, 1998; Usher, Cohen, Haarmann, & Horn, 2001) and for binding together different features of one maintained item (Hummel & Holyoak, 2003; Raffone & Wolters, 2001). Such models successfully generated numerous predictions later supported by neuroimaging (e.g., Edin et al., 2009; Jensen & Lisman, 1998; Raffone & Wolters, 2001), and also showed why temporary bindings are so crucial for complex cognition. It is so because they allow to flexibly represent and transform the arbitrary relational structures (Hummel & Holyoak, 2003; Oberauer et al., 2008).

Crucially, some oscillatory models (Hummel & Holyoak, 2003; Jensen & Lisman, 1998; Raffone & Wolters, 2001; Usher et al., 2001) naturally explain the limit in WM capacity as an emergent property of PM, which results from the trade-off between the number of to-be-maintained representations versus the ability to distinguish among them. As brain uses temporal coding for separating representations in PM, and time is a limited resource, brain is not able to crowd too many oscillations into one interval, because they start to overlap and so they stop being distinctive.

On the contrary, models which do not rely on oscillations, in a more arbitrary way assume that a limit is exerted on the number of PM's slots (e.g., Kahana, 1996) or the amount of PM's activation (e.g., Daily, Lovett, & Reder, 2001), so no natural capacity limit is identified by those models. Similarly, models which use only one cycle of activation change to code an item (e.g., Botvinick & Plaut, 2006; Davelaar, Gosher-Gottstein, Askenazi, Haarman, & Usher, 2005) seem to be less neurally and functionally plausible than the full-fledged oscillatory models. For example, the former are unable to show that whether monkey responds correctly or not to the WM task depends on whether neuronal firings in monkey's cortex are desynchronized or not (Siegel, Warden, & Miller, 2009), nor that the human WM capacity depends on the number of gamma oscillations occurring within one theta phase (Kamiński, Brzezicka, & Wróbel, 2011) — two observations that can be easily explained on grounds of a full-fledged oscillatory model (Jensen & Lisman, 1998).

Although the oscillatory models nicely explain how brains handle maintenance in PM, and they give important insights into the nature of capacity limits, no such model has yet tried to explain the reason for the fact that *people differ in capacity*. Though in principle all of us could have had the maximum possible capacity, in fact individual capacity hugely varies among humans, and it severely limits intellectual abilities of a substantial part of the population.

This paper presents a novel, neurobiologically plausible model of PM which aims to demonstrate which features of a possible oscillatory mechanism of PM are responsible for observed individual differences in capacity. Firstly, we test if a systematic manipulation to one model's parameter, specifically the strength of lateral inhibition applied among memory items, can replicate the distribution of capacity estimates in the population, as well as a number of more specific effects related to capacity. Moreover, in a subsequent zero-parameter cross-task simulation, using individual estimates of inhibition related to our participants' PM, we intend to replicate the individual differences in performance within a more complex task of relational integration, which requires detecting a predefined abstract relation in a pattern of stimuli. As such a task is known to strongly predict fluid reasoning (Chuderski, Taraday, Necka, & Smolen, 2012; Oberauer et al., 2008), the replication of individual effectiveness of relational integration with the oscillatory model will constitute one step towards linking lower-level neuronal mechanisms of PM to higher-level cognitive processing.

2. Oscillatory model of primary 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 (e.g., an object's attribute, a concept, a word, etc.). Like in many other models, a level of internal activation x_i is assigned to each element i.

The external output y of the element i in time t has been defined using a commonly applied sigmoid function of x_i, according to the following formula (1):

$$y_i(t) = \frac{1}{1 + \exp\left(-\delta\left(x_i(t) - \frac{1}{2}\right)\right)}. \tag{1}$$

The parameter δ controls the level of nonlinearity of the relation between y and x. For the small δ values, this relation for $0 < x < 1$ is almost linear. With increasing δ, (1) gradually moves into a threshold function with the threshold at $x = .5$. This function is primarily responsible for a neurally plausible shape of oscillations, but it has no direct role in determining the model's capacity.

In order to express the presumed mechanism responsible for binding together the features of one item, while keeping the different items separated, we introduced a new equation (in comparison to other existing oscillatory models) which controls changes in the level of activation of ith element (2):

$$x_i(t+1) = x_i(t) + \frac{\lambda}{1+y_i(t)} + \alpha\sum_k \exp(x_k(t) - x_i(t)) - \beta\sum_j \exp(x_j(t) - x_i(t)) + \epsilon(n). \tag{2}$$

The parameter λ controls how much the element i is autoactivated by the recurrent connections feeding its output back. That mechanism reflects a commonly postulated self recurrent nature of neuronal groups in brain structures underlying the focus of WM attention (O'Reilly & Munakata, 2000). The parameter λ primarily regulates the frequency of oscillations, but it has no significant influence on the model's capacity.

The index k denotes elements which output just before element i does, namely those in $[y_i, y_i + \kappa]$ range. As a result, the parameter α determines how much the outputs of elements which oscillate close to the element i will increase its activation. This accounts for the known fact that neurons which fire in synchrony with a given neuron, but not those that fire in distinct time windows, strongly influence its potential. Such a mechanism of coactivation helps to maintain synchrony among items yielding similar outputs, and its strength (α) is a candidate for the determinant of the model's capacity. The parameter κ defines the temporal resolution of bindings: the larger κ, the more distant (in terms of activation) elements will be considered by the model as bound within the same representation, specifically those in the $[y_i - \kappa, y_i + \kappa]$ range. Low values of κ (between .03 and .07) do not influence the model's capacity, so in subsequent simulations κ was set to .05.

The index j denotes elements which are not k nor i elements, that is, those that fall out of the above range. These elements encode representations separate from a representation encoded by the elements i and k. The parameter β controls the strength of inhibition exerted by elements j, which decreases the activation of element i. How much the element j inhibits the element i depends on a difference in the elements' activity: a relatively more active element will inhibit the element i more strongly than will inhibit a less active element. β is the main candidate for a parameter controlling the capacity of our oscillatory model.

The last part of (2) consists of the noise ϵ, drawn from the normal distribution with the mean equal to zero, and the variance dependent on the parameter n. The noise negatively influences capacity, but for the sake of simplicity, in the subsequent simulations it has been turned off ($n = 0$).

The activations and external outputs of elements are updated in discrete cycles. Each cycle represents a period of several milliseconds, though the precise timings of the model's operation are not analyzed in this paper. As soon as the output of an element approaches unity (this reflects firing of a neuronal group), the parameter λ for that element is temporarily changed to a negative value, which makes this element quickly fall below a base level of activation (set to .2). This is meant to reflect the well-known phenomenon of refraction. Then, the value of λ is reset to a default value and the element starts building up its activation above the base level. However, inhibition signals may be so strong that the activation may decrease below zero — the value adopted as a minimal activation necessary to stay in the buffer — and in such a case an element may permanently fall out of PM.

Generally, the number of elements which can be bound together within one synchronous oscillation is not limited. However, in the following simulations we apply only pairs of synchronized elements (an item identity and its position).

3. 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., a letter and its temporal or spatial position, see below) 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 $1 - 4\kappa$, and those subsequent pairs are added at a level of $x = x_{max} + \kappa + (1 - x_{max})/2$, 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.

In the model, the capacity limit arises because the addition of consecutive pairs increases the strength of total inhibition that each pair receives. When the total inhibition surpasses the results of autoactivation (regulated by the parameter λ) and coactivation (governed by the parameter α), 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 will also fall out drastically increases. Thus, the parameter β is the main determinant of the model's capacity. The higher β, the faster the elements start falling out of the buffer. So, the model predicts that a maximum capacity will be achieved when there is no inhibition at all ($\beta = 0$). Indeed, in such a case, the model was able to maintain twelve pairs, surpassing human capacity. In more realistic cases, 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 most appropriate values of β reflect the trade-off between low inhibition (many elements can be maintained, but they are unbound) and high one (less elements can be maintained, but they are properly bound).

By gradually increasing the moderate value of β, we replicated the highest capacity (around five items) that is observed among people (see the next section), mean capacity (around three items), and the lowest possible capacity (only one item). Patterns of oscillations for each capacity level are presented in Fig. 1.

Although β is the most important determinant of the model's capacity, three other parameters can in principle modulate workings of the model. Firstly, the increase in

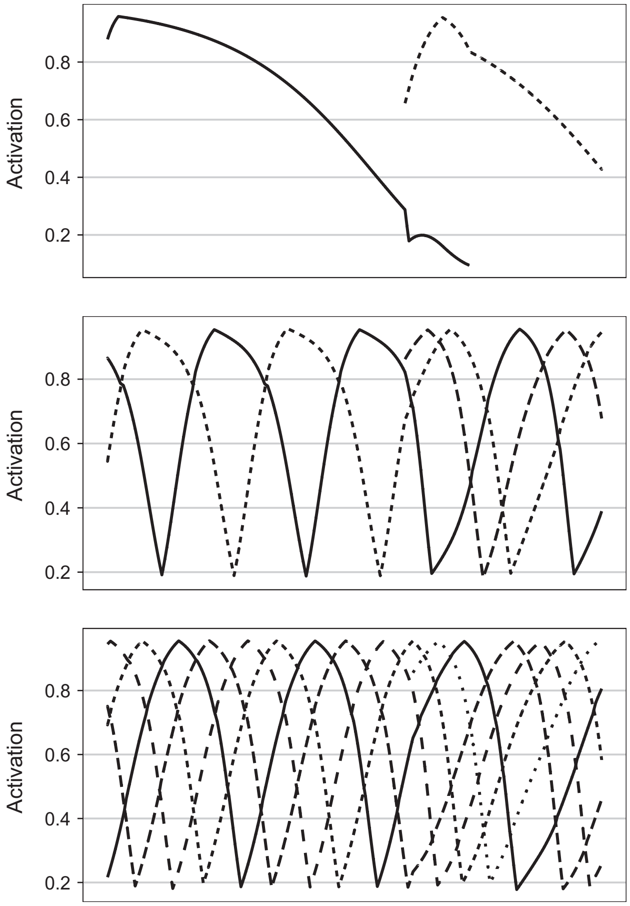

Fig. 1. Patterns of oscillations for the lowest (=one item; upper panel), medium (=three items; middle panel), and largest (=five items; bottom panel) model's capacity. When capacity is insufficient, the addition of a new pair eliminates an existing pair (see upper panel).

α parameter would strengthen synchrony of bound elements. Such a mechanism may reflect a top-down boosting applied by the prefrontal cortex, which can pass additional activation to PM (see Edin et al., 2009). This extra boosting causes stronger activation between elements. However, because we assume that a given element, when fires, can activate only elements firing in its temporal proximity, we expect that the boosting influences only the coactivating elements. Another, more technical factor which can impact capacity is the level of noise (n). The higher noise, the higher the probability that errors will aggregate through time and the pairs will become desynchronized. The last parameter potentially related to capacity is the value of κ. If κ is too large, then the pairs are stable, but there is little "room" for adding new pairs and the capacity will be low. If κ is too low, then many pairs could be added, but even tiny differences in paired elements' activity can cause desynchronization between them.

4. Measurement and simulation of individual differences in primary memory capacity

In the following simulations, we set the α parameter to a low value of .0001, which resulted in relatively weak influence of coactivation on the model's performance. The parameter λ was drawn from the normal distribution with $\mu = .05$, and $\sigma = .005$. So, together with the κ parameter, we set four global parameters. In order to replicate the distribution of PM capacity as observed in a sample of participants, we individually varied the values of β (see below).

4.1. Basic effects regarding primary memory

The first task which we modeled was the well-known Sternberg task. A version of the task used in our study consisted of the serial presentation of six letters randomly drawn from a set of 18 consonants. A seventh letter, shown after a mask, was a probe that could either match one of the letters or be different from them. The correct answer was to accept a matching probe but to reject a differing one. The model attempted to add to its own buffer six letter-position pairs, and then a probe in a particular position was presented. The model ran two processes which tested: (a) whether the element identical to the probe could be found in the buffer and a position bound to it (if any) matched the position of the probe or not, and (b) whether the element identical to the probe's position could be found and an element bound to it matched the probe's identity or not. If either the identity or the position had been found, and its binding matched either the probe's position or identity, respectively, then the model generated a positive answer. If both elements had been found, but one of them did not match the corresponding element, the answer was negative. If no element had been found, the model guessed either the positive answer with a probability ρ (decisional bias) or the negative answer with a chance $1 - \rho$.

We started testing our model by checking if it is able to replicate the recency effect, which is a phenomenon commonly found in WM studies. Moreover, when WM performance relies primarily on PM, as for example in tasks applied with fast presentation rate, usually there is no primacy effect (Chuderski, Stettner, & Orzechowski, 2007). The simulated recency effect and no primacy are shown in Fig. 2 (note that in this and all subsequent figures, the errorbars reflect 95% confidence intervals).

A more interesting observation — in light of the aims of this paper — regards the fact that people quite effectively use positional information to reject distractors presented to them. For example, one of us (Chuderski & Stettner, 2012, Exp. 1, a positive digit condition) used a modified Sternberg task which was analogical to the standard version, with one exception that a probe was accompanied by a digit, which denoted the letter's position in a memory set. The digit could match the target's position or not, and the task of 47 participants was to accept only matching digits. We observed that participants correctly accepted more matching digits ($M = .78, SD = .11$) than incorrectly accepted non-matching ones ($M = .26, SD = .17$). This result suggests that people effectively maintained the positions of items in WM. Results of 47 corresponding simulations were close to observations: the model accepted

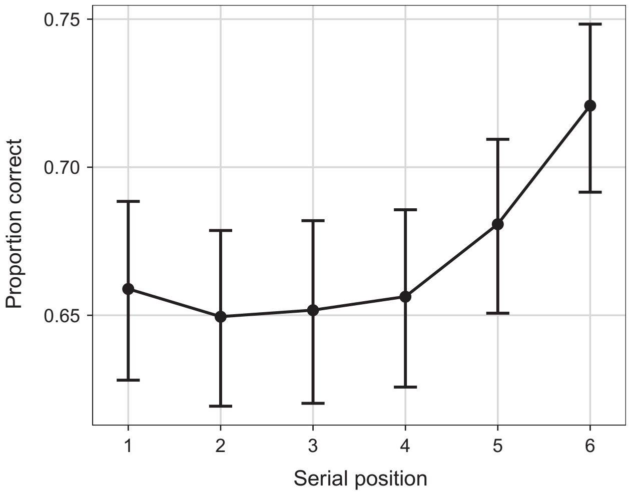

Fig. 2. Accuracy of the model for all serial positions in the six-item Sternberg task.

$M = .67$ of the matching digits, while it did not reject only $M = .33$ of the to-be-rejected digits. Slightly lower accuracy of the model resulted from the fact that it solely used its PM, while people most probably relied their performance on both PM and SM. This result indicates that a proper PM model must account for binding of the representations to their contexts. Unbounded representations often are simply useless.

4.2. The distribution of primary memory capacity

The crucial simulation consisted of the replication of the distribution of PM capacity estimates observed in the sample of 168 young adults, who fulfilled a two-array comparison task (Luck & Vogel, 1997). The task is assumed to require maintenance of material in PM, while SM barely helps in this task due to the use of figural material and a fast presentation rate. Ten other participants were excluded from the original data (reported in Chuderski et al., 2012) because their results suggested that they were not able to maintain even one item in their PM.

The original task required memorizing an array of a few items. Then, after a retention interval, the array was repeated, but there was 50% chance that exactly one item was changed. No other item could be altered or moved to another location. The task was to indicate if the item had changed or not. We used a version of the task consisting of a single-probed recognition: one of the items in the second array was surrounded by a cue indicating that if any of the items was changed, it was the surrounded one. If no item was changed, the cue indicated a random item. The test included 90 trials. Each self-paced trial consisted of a virtual, four by four array filled on random with four, five, or six (i.e., set size) stimuli drawn from a pool of 16 simple black figures (e.g., a square, a circle, a rhombus, an arrow, a cross, etc.), each approximately 2.5 × 2.5 cm in size. The array was presented for 0.5 s multiplied by its set size.

An estimate of PM capacity uses the proportion of correct responses for arrays with one item changed (hits; H) and the proportion of incorrect responses for unchanged arrays (false alarms; FA). PM capacity is estimated to k items (out of N items of the set size), on the assumption that a participant produces a correct hit or avoids a false alarm only if a cued item is transferred to his or her PM (with the k/N chance). If a non-transferred item is cued, then the answer is guessed. Thus, the sheer PM capacity is equal to $k = N(H - FA)$. The value of k is believed to approximate the actual number of items held in PM by individuals (Rouder, Morey, Morey, & Cowan, 2011).

We used an analogous model as for the Sternberg task, with an exception that this time it encoded figures and their spatial positions. The value of $\beta = .0026$ was found to optimize the mean k value in the sample ($M\ k_{sim} = 3.01, M\ k_{obs} = 2.92$). In order to simulate 168 individual results, we varied the values of parameter β for each individual simulation, by drawing it from the normal distribution with $\mu = .0026$ and $\sigma = .0004$. Histograms of the observed and simulated distributions of the k value are presented in Fig. 3. Both distributions did not differ significantly ($\chi^2(7) = 6.81, p = .45$) and the respective R^2 value (.94) was satisfactory. In order to more precisely measure the level of similarity between the observed and simulated distributions we used Kullback–Leibler divergence statistics. The Kullback–Leibler divergence between observed and simulated distributions was .074. This measure is a logaritmic, weighted difference between normalized areas of continuous probability distributions. The measure can take minimal value of zero, when two distributions overlap and there is no difference between their masses. The measure increases when there is high probability that a value

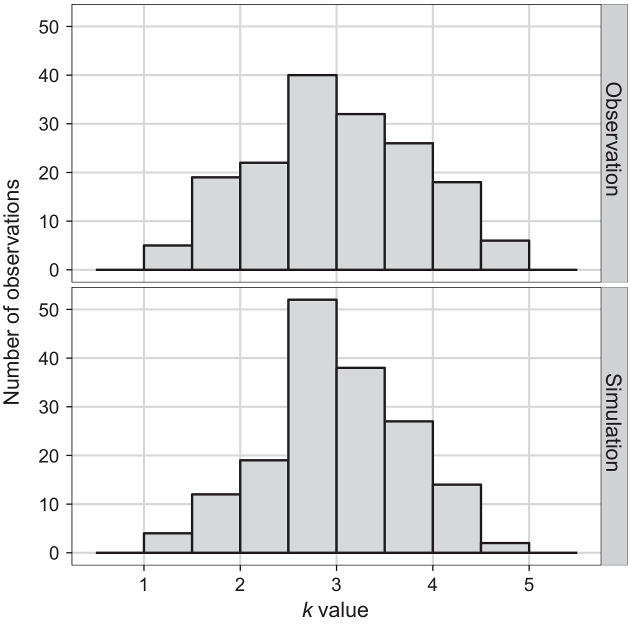

Fig. 3. The number of observations (upper panel) and simulations (lower panel) yielding particular values of k.

occurs in a given distribution, while there is low probability of its occurrence in a compared distribution. Value of .074 means that mass of the weighted logaritmic difference between the observed and simulated distributions is only 7.4% of mass of each of the distributions alone, and can be considered a very small difference.

5. Experimental effects related to capacity

Next, we examined if there were any specific differences in performing the task related to the differences in participants' capacity, and whether the model was able to replicate them. An analysis of the observed data indicated that participants more accurately responded to unchanged arrays than to changed ones. In the model, this was accounted for by setting ρ value to .43. As highly capacious participants would rarely guess (all necessary information was in their PM), we expected that the difference between accuracy in both conditions should diminish with the increasing k value. This effect has indeed been found in both observed and simulated data (see Fig. 4). We also predicted that the discrepancy in accuracy between changed and unchanged arrays should increase as N increases. Such a pattern has also been present in the observed data (see Fig. 5). However, though the model aptly replicated the mean accuracy, it overpredicted accuracy in the four-item and five-item conditions, while it underpredicted accuracy in the six-item condition.

In search for a possible cause of the mismatch, we investigated if it may be related to the differences in capacity. We compared the k values for the respective item conditions between both participants and simulations yielding high versus low k estimates ($k > 3.5$ versus $k < 2.5$). We found that in the case of highly capacious participants, the k estimate significantly increased with N, $\Delta k_{4,6} = .85$, 95%CI = [.58, 1.12], while in the case of the low-capacity group the k value was significantly lower in the six-item condition than in the five-item one, $\Delta k = -0.37$, 95%CI = [−0.09, −0.64] (see Fig. 6, left panel). The former effect is a direct consequence of the fact that the k estimates of many high-capacity participants equaled or surpassed four items, so the k values in the four-item condition might underestimate their capacity. In fact, when only the six-items condition was considered, the maximum human

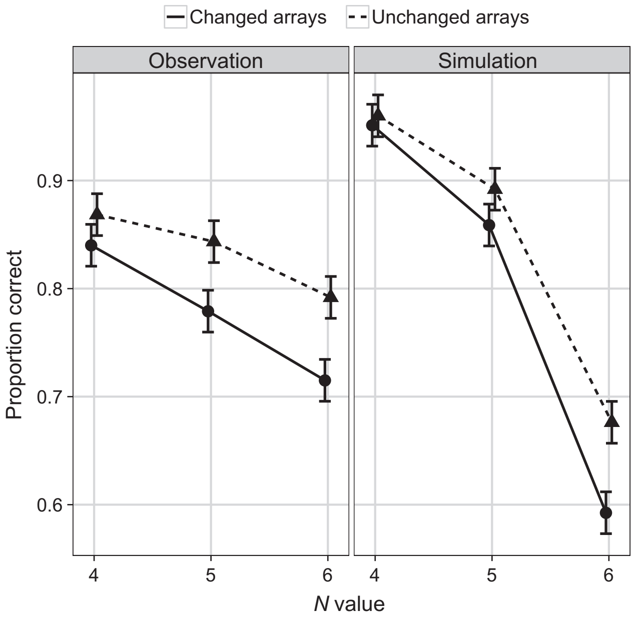

Fig. 5. Accuracy in the changed and unchanged array conditions, in the function of the set size (N).

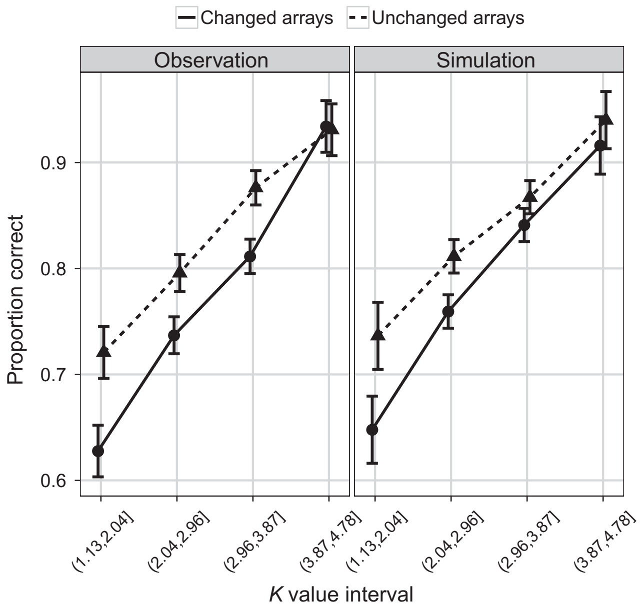

Fig. 4. Accuracy in the changed and unchanged array conditions, in the function of the k value.

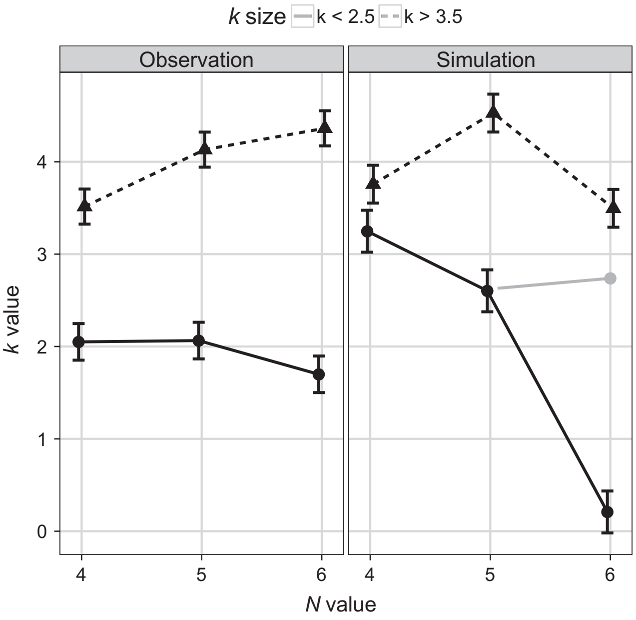

Fig. 6. The mean values of k in the function of set size, for low-capacity (total $k < 2.5$) and high-capacity ($k > 3.5$).

capacity was $k = 5.6$, and it has been accounted for by the model. The latter effect is much more interesting: it indicates that PM of low capacity people was even less effective than usual if the discrepancy between their actual capacity and the imposed requirements increased. This result is coherent with other behavioral and neuroimaging data (e.g., Todd & Marois, 2004).

The analysis of how the model coped with the increasing N, depending on the adopted value of β, showed qualitatively similar pattern of data (see Fig. 6, right panel), though there was a large quantitative difference in comparison to observations. Increasing the N value was on average not disruptive to the model's capacity in the case of low values of lateral inhibition, while the model dramatically decreased its capacity when the level of inhibition was high.

What could be responsible for such a profound discrepancy between participants and simulations regarding individual k values in the case of the six-items condition and the low capacity? Edin et al. (2009) suggested that when memory load largely exceeds one's capacity, an additional top-down activation is recruited by the brain in order to counteract the lateral inhibition surpassing the brain's capability of dealing with it. Maybe too weak coactivation applied in our model was the cause of the above discrepancy? We tested this hypothesis by re-running the six-item condition for the low capacity group with the doubled α value (.0002) in comparison to the original simulation. In result, the model's accuracy highly increased, and our data better fitted human data (see Fig. 6, right panel, gray line). Thus, it is not the case that in our simulation the coactivation was underestimated in general (definitely not in the $N = 4$ and $N = 5$ conditions), but it was insufficient only when memory load largely exceeded the model's resources to cope with it.

6. Individual differences in relational integration

So far, we have identified one possible constraint on the individual capacity of PM. However, another important research question is: why precisely such a limit also constrains higher-level cognition? According to Halford, Cowan, and Andrews (2007), the link between PM capacity and higher-level cognition arises because that capacity influences the number of relations that can be set between actively maintained items. Furthermore, Oberauer et al. (2008) proposed that constructing those new relations depends on the ability to set flexible, temporary bindings between items held in PM and their corresponding positions within some mental structure, like abstract placeholders in the proper schema or solution's representation. Due to the effective binding of items to their roles within a relation, a person may be able to integrate relations crucial for deductive reasoning (e.g., integration of premises into mental models; Johnson-Laird, 2006), inductive thinking (e.g., mapping elements of source and target during analogy-making; Hummel & Holyoak, 2003), and problem solving (even creative; Wiley & Jarosz, 2012).

We aimed to test if the variation in lateral inhibition within our model can reproduce the individual differences in relational integration, observed among our participants. To measure relational integration, we used the relation monitoring task (Oberauer et al., 2008). The task consisted of the presentation of 80 patterns. Each pattern consisted of a three by three array of two-letter syllables, presented for 6 s. Only 20 patterns included three syllables ending with the same vowel, located in one row, column, or diagonal line. This was a simple predefined relation that participants were instructed to look for. Two subsequent arrays could differ by exactly one syllable; a short "blink" of the array indicated that a syllable had been substituted. Accuracy of relational integration was calculated as a number of correct responses for the specified relation minus one third of false alarm errors (as three times more non-target patterns occurred than target patterns). The same sample of 168 people was tested.

The model of the task assumed that people systematically encode in their PM as much syllables as they can, and then seek for the target relation among them. Each syllable in PM was bound by a synchronized oscillation to a tag that informed about its location within the matrix, which was crucial for searching of the relations. The model searched for them sequentially, first in rows, then in columns, and finally in diagonal lines. Every test of relation consisted of two steps: (a) check if the last vowels of two examined syllables do match, and if yes (b) test if the third element also does satisfy that condition. If the second stage gave the positive result, then the search was stopped and a response was generated. If it did not, a next row, column, or diagonal line was processed until a next pattern occurred. The model's capacity was crucial for performance, because, for example, holding in PM only two neighboring syllables allowed it to test only one row/column/diagonal line, while maintaining four syllables located within a square allowed the model to compare two rows, two columns, and one diagonal line at the same time.

In the model of the monitoring task, we used the same values of parameters as in the previous simulation. Especially, we used the same 168 individual values of the β parameter. The only additional parameter was the speed of perceptual search, as it was a specific feature of the monitoring task. The observed and simulated distributions of relational integration accuracy are presented in Fig. 7. The means of the former (.74) and the latter (.73) distribution closely matched, and the fit between the two was very good, $\chi^2(9) = 5.25$, $p = .81$, $R^2 = .84$. The Kullback–Leibler divergence between observed and simulated distributions was .052.

Moreover, we replicated the strength of correlation between the k value and relational integration accuracy in the observed and simulated participants (in the case of the latter, we treated the same values of β in both models as denoting the same participant), $r_{obs} = .33$, $r_{sim} = .41$. The relationships between the β and k values, between the β and relation integration accuracy, and between the

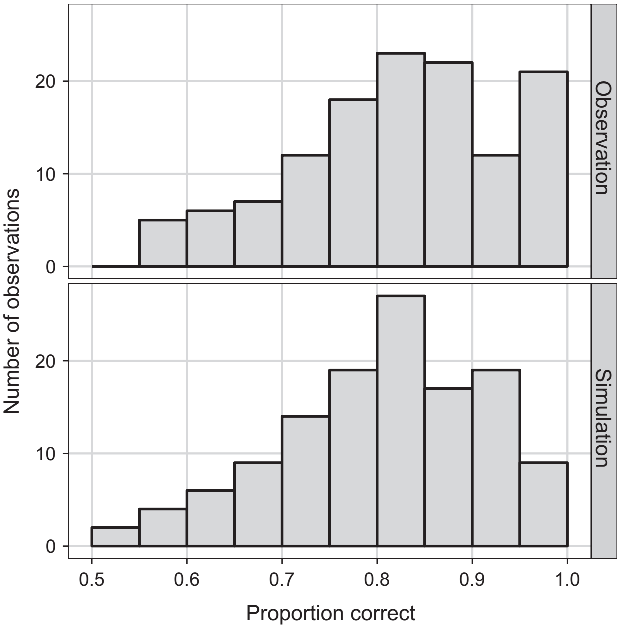

Fig. 7. The number of observations (upper panel) and simulations (lower panel) yielding particular values of relation integration accuracy.

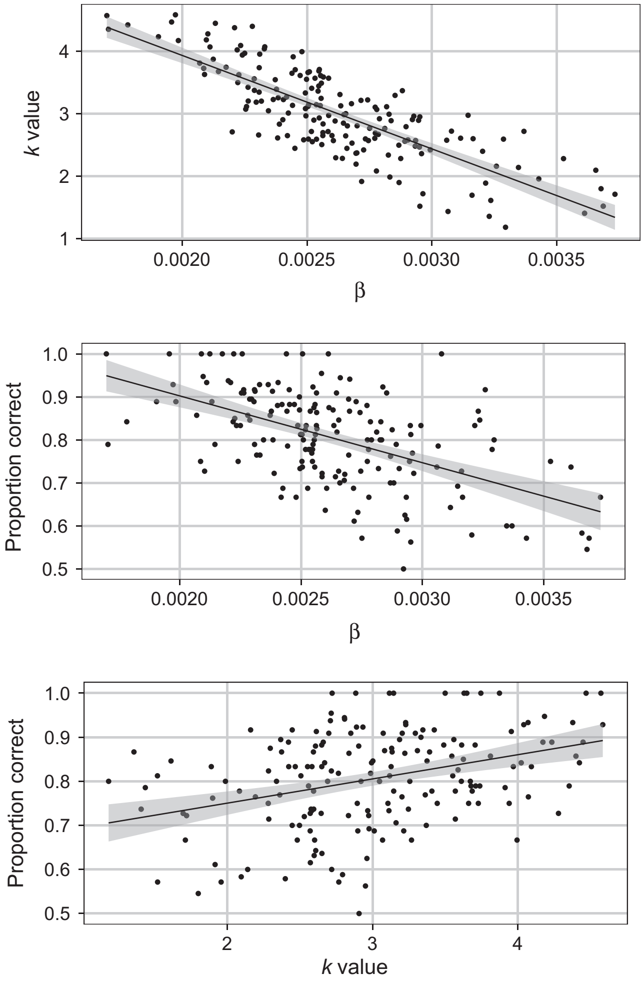

Fig. 8. Scatter plots and regressions for the β and k values (upper panel), the β and integration accuracy (middle panel), and the k value and integration accuracy (bottom panel).

k value and integration are shown in Fig. 8. It is worth noting that the former depended on β less deterministically than did the latter, and both variables intercorrelated only moderately.

7. Discussion

Using a novel oscillatory model, which was aimed to reflect the mechanisms of active maintenance of information in the parietal cortex, we have demonstrated that the variation in the strength of lateral inhibition among oscillating representations, which was necessary for temporal separation of bindings underlying those representations, can explain the individual differences in PM capacity in the large sample of participants. In our sample, that capacity varied from one item up to almost six items (i.e., when $N = 6$), that is, as predicted by Cowan (2001). This result seems to pose a problem for those oscillatory models which predict that WM capacity is fixed to only four items (e.g., Raffone & Wolters, 2001). Most probably, those models would not be able to match the full distribution of WM capacity in the human population.

However, the story regarding the replication of individual differences in capacity with the use of lateral inhibition was not that simple. A more precise analysis of the effects of memory load in the function of individual capacity showed that the strength of lateral inhibition is not the only factor influencing the model's capacity. When the model attempted to maintain too many items in relation to its actual capacity, this fact increased the inhibition to such a high level that it led to a catastrophic decrease in capacity. In line with others (e.g., Edin et al., 2009; Todd & Marois, 2004), we suppose that the main role of the prefrontal cortex in active maintenance of information is to prevent such situations by additionally activating PM in a top-down manner. In our model, this was done by adjusting the coactivation of elements oscillating together. The analysis of computational properties of the coactivation, and the search for the α values enhancing the fits of the model should be the subject of our future investigations.

Moreover, the same oscillatory mechanism that limited the number of maintained items in the WM task, also determined the accuracy of relational integration, as displayed by an example task which required monitoring of the simple relation among syllables. As the process of relational integration is presumably crucial for various complex intellectual processes, our result identifies a novel possible link between neurally plausible oscillatory brain mechanisms and higher-order cognition (for another proposal in this regard see Hummel & Holyoak, 2003).

Summing up, we presented a preliminary but highly original computational study devoted to the examination of neurocognitive mechanisms underlying the individual variation in both PM capacity and relational integration. Its results suggest that the concepts of oscillations and bindings can have a great explanatory power in regard to both working memory and higher-order cognition.

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