Adaptive chunking improves effective working memory capacity in a prefrontal cortex and basal ganglia circuit

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Abstract

How and why is working memory (WM) capacity limited? Traditional cognitive accounts focus either on limitations on the number or items that can be stored (slots models), or loss of precision with increasing load (resource models). Here we show that a neural network model of prefrontal cortex and basal ganglia can learn to reuse the same prefrontal populations to store multiple items, leading to resource-like constraints within a slot-like system, and inducing a tradeoff between quantity and precision of information. Such "chunking" strategies are adapted as a function of reinforcement learning and WM task demands, mimicking human performance and normative models. Moreover, adaptive performance requires a dynamic range of dopaminergic signals to adjust striatal gating policies, providing a new interpretation of WM difficulties in patient populations such as Parkinson's disease, ADHD and schizophrenia. These simulations also suggest a computational rather than anatomical limit to WM capacity.

Keywords: working memory, effective capacity, information compression, prefrontal cortex, basal ganglia, reinforcement learning, dopamine

Introduction

It has long been appreciated that working memory (WM) capacity is limited, but despite many decades of research, the nature of these limitations remains controversial. For example, early work by Miller (1951) famously posited that WM is limited to roughly 7 items, but he also stated that the precise limitation might vary depending on information quantity of the relevant memoranda. More recently, a vigorous debate over the last two decades has divided roughly into two schools of thought. The "slots" theory argues that WM is limited to a specific number of items. According to this account, each item is stored in a discrete slot and encoded with high precision, leading to low or zero errors when that item is probed at recall. When the number of items to be remembered exceeds the capacity (roughly 4 items; Cowan (2008)), some items will be forgotten, and therefore participants resort to guessing (Fukuda, Awh, & Vogel, 2010; Luck & Vogel, 2013; W. Zhang & Luck, 2008). In contrast, the "resource" theory argues that people can store an arbitrarily large number of items in WM, with no inherent item limit, but that each item competes for a shared pool of resources. As a result, the precision of each memoranda goes down with each added item to be recalled. In the limit, when many items are presented, each one is recalled with low precision, which can masquerade as guessing(Bays, Catalao, & Husain, 2009; Ma, Husain, & Bays, 2014).

Critically, regardless of the distinction between discrete and continuous resources, the measured WM "capacity" from experimental data is not fixed. For example, individual differences in WM capacity are largely determined not by the raw number of items one can store but rather one's ability to filter out distracting items ((Astle et al., 2014; Feldmann-Wüstefeld & Vogel, 2019; McNab & Klingberg, 2008; Vogel, McCollough, & Machizawa, 2005)). More generally, one can leverage various (potentially unconscious) memory strategies to improve "effective capacity", leading to experimentally observed capacity measurements that fluctuate depending on stimulus complexity, sensory modality, and experience with the stimuli ((Pusch et al., 2023)). Thus a key but often overlooked aspect of WM lies in the efficient *management* of access to

and from working memory. Taking into account this management may also provide a mechanism for understanding WM not only in terms of maintenance, but also how gating strategies may be used for manipulation of information – i.e., "working with memory" (Moscovitch & Winocur, 2009). In other words, **effective capacity** encompasses gating items into/out of WM as well as the maintenance of items.

For example, recent theoretical and empirical work suggested that information stored in WM can be partitioned into discrete representations, but that similar items could be stored in a shared partition, in effect chunking them together (Nassar, Helmers, & Frank, 2018). Intuitively, it is simpler to remember that one needs to purchase dairy items, bread, and fruit rather than to remember to buy milk, cheese, bread, oranges, and bananas. This active chunking strategy serves as a lossy information compression mechanism: it frees up space for other items to be stored and recalled. This happens at the cost of reducing precision for the chunked items. Experimental evidence provided support for such a model over alternatives, and provided a mechanism to explain why precision can be variable across trials as posited by previous resources models (Berg, Shin, Chou, George, & Ma, 2012). Moreover, (Nassar et al., 2018) showed that the optimal chunking criterion (i.e., how similar two items need to be to merit storing as a single chunk) varies systematically with set size (number of items to be remembered) and can be acquired via reinforcement learning (RL). In line with this account, they reported evidence that humans adapted chunking on a trial by trial basis as a function of reward feedback in their experiment. They also performed a meta-analysis of other visual working memory (VWM) datasets showed that optimal performance was associated with more chunking with increasing set size. Thus, at the cost of small errors (due to loss in precision), normative models and humans have overall better recall and performance when employing this chunking method. This and related theories (Brady & Alvarez, 2011, 2015; Brady, Konkle, & Alvarez, 2011; Nassar et al., 2018; Swan & Wyble, 2014; van den Berg, Awh, & Ma, 2014; Wei, Wang, & Wang, 2012) may reconcile differences between the slots and resources theories.

While these normative and algorithmic models are consistent with experimental data, it is unclear how *biological* neural networks could perform such adaptive and flexible chunking. If a biological neural network exhibits the same mechanism, we can make more clear predictions about human WM as well. The dominant neural model of visual working memory is the ring attractor model of prefrontal cortex (PFC), whereby multiple items can be maintained via persistent activity in attractor states (Edin et al., 2009; Nassar et al., 2018; Wei et al., 2012). In these models, nearby attractors coding for overlapping visual stimuli can collide, leading to a form of chunking and loss of precision, and where some items are forgotten due to lateral inhibition (Almeida, Barbosa, & Compte, 2015; Nassar et al., 2018; Wei et al., 2012). While these models have successfully accounted for a range of data, by modeling only the PFC (or a single cortical population), they have limitations. Firstly, these models cannot determine whether or not an item should be stored. In other words, unlike humans (McNab & Klingberg, 2008; Vogel et al., 2005), they cannot improve effective capacity by filtering content to only include relevant information. Secondly, any chunking that occurs in these models is obligatory – determined only by how overlapping the neural populations are and hence whether attractors will collide. Thus, chunking can't be adapted with task demands as in normative models and human data (Nassar et al., 2018). Finally, during recall, these network models cannot select a specific item from memory based on a probe (accuracy in these models is considered high as long as the relevant stimulus is encoded somewhere in the pool of neurons; (Almeida et al., 2015; Edin et al., 2009; Wei et al., 2012)). In other words, these models have no way of manipulating or accessing the contents of the WM.

Another complementary line of biologically-inspired neural network models addresses how interactions between basal ganglia (BG), thalamus, and PFC support independent updating of separable PFC "stripes" (anatomical clusters of interconnected neurons that are isolated from other stripes; (Frank, Loughry, & O'Reilly, 2001; Levitt, Lewis, Yoshioka, & Lund, 1993; Pucak, Levitt, Lund, & Lewis, 1996). These prefrontal cortex basal ganglia working memory (PBWM) models focus on the aforementioned "management" problem. They simulate the brain's decision whether to encode a sensory item in WM ("selective input gating"). They also simulate which item (of those stored in WM) should be accessed ("output gating") for reporting or subsequent processing (Hazy, Frank, & O'Reilly, 2007; Kriete, Noelle, Cohen, & O'Reilly, 2013; Krueger & Dayan, 2009; O'Reilly & Frank, 2006; Stocco, Lebiere, & Anderson, 2010; **?**). The combination of input and output gating decisions that are made can be summarized as the *g*ating policy. Via dopaminergic reinforcement learning signaling in the BG, the networks learn an effective gating policy for a given WM task (Frank & Badre, 2012). This policy includes (i) whether or not to store an item (i.e., if it is task-relevant or distracting), (ii) if relevant, in which population of PFC neurons to store it, and (iii) which population of PFC neurons should be gated out during recall or action selection. As such, PBWM networks can perform complex tasks that require keeping track of sequences of events across multiple trials while also ignoring distractors. The PBWM framework also accords with multiple lines of empirical evidence, ranging from neuroimaging to manipulation studies, suggesting that the BG contributes to filtering (input gating) of WM (which improves effective capacity) (Baier et al., 2010; Cools, Miyakawa, Sheridan, & D'Esposito, 2010; Cools, Sheridan, Jacobs, & D'Esposito, 2007; McNab & Klingberg, 2008; Nyberg & Eriksson, 2016)

and selecting among items held in WM (output gating; (Chatham, Frank, & Badre, 2014)). Evidence also supports the PBWM prediction that striatal DA alters WM gating policies analogous to its impact on motor RL (Frank & O'Reilly, 2006; Moustafa, Cohen, Sherman, & Frank, 2008); for review see (Frank & Fossella, 2011). Finally, these human studies are complemented by causal manipulations in rodent models implicating both striatum and thalamus as needed to support WM maintenance, gating and switching (Nakajima, Schmitt, & Halassa, 2019; Rikhye, Gilra, & Halassa, 2018; Wilhelm et al., 2023). However, to date, these PBWM models have only been applied to WM tasks with discrete stimuli and thus have not addressed the tradeoff between precision and recall in VWM. Due to the discrete nature of the stimuli, accuracy is typically binary, and WM information could not be adaptively chunked. Further, previous PBWM studies only trained and tested within the allocated capacity of the model, limiting the application to common human situations in which set size of relevant items goes beyond WM capacity.

In sum, these two classes of neural WM models address complementary phenomena but their intersection has not been studied. In particular, how can our understanding of BG-PFC gating inform the slots vs resources debate and the nature of WM capacity limits more generally? On the surface, PBWM is a slots model: it has multiple, isolated PFC "stripes" that can be independently updated and accessed for read-out. Note, however, that performance is improved in these models when they use distributed representations within the stripes (Hazy et al., 2007; Kriete et al., 2013), which can have resource constraints (Frank & Claus, 2006). We thus considered whether PBWM could acquire, via reinforcement learning, a gating strategy whereby it stores a "chunked" representation of multiple items within the same stripe, leaving room for other stripes to store other information and *in effect increasing the effective capacity without increasing the allocated capacity.*

Here, we sought to combine successful aspects of both models. We considered whether PBWM could be adapted to perform VWM tasks with continuous stimuli and whether it can learn a gating policy via RL that would support chunking to meet task demands. We include a ring attractor model that allows for mergers of continuous-valued stimuli via overlapping representations (Almeida et al., 2015; Edin et al., 2009; Nassar et al., 2018; Wei et al., 2012). But rather than representing all input stimuli at once, the network evaluates a single sensory input in the context of stimuli already stored in one or more PFC stripes. The ring attractor can then merge or chunk the sensory input with its nearest neighbor in PFC. Importantly, the resulting chunks are not obligatorily stored in WM. Rather, the BG learns a gating policy so that it can potentially store the original (and more precise) sensory input, or it can replace a currently stored representation with the chunk – and adaptively alter its strategy as a function of task demands (set size). During recall, the network can gate out the corresponding (original or chunked) representation linked to the probe, and reproduce hallmarks of human performance in continuous report VWM tasks.

Notably, we find that this chunk-augmented PBWM network outperforms control models that lack chunking abilities across a range of task conditions. Chunk models outperform control networks even when the control models are endowed with an allocated capacity that exceeds set size. This latter result stems from a credit assignment problem that arises when networks must learn to store and access multiple items in WM. Chunking instead allows for a common set of stripes to be repeatedly reused and reinforced, limiting the number of possible solutions explored. As such, this result lends insight into a normative rationale for why WM capacity is limited in the first place. Finally, these performance advantages depend on a healthy balance of BG dopamine signaling needed to support adaptive gating policies that enhance effective capacity, providing a novel account for WM deficits resulting from aberrant BG DA signaling in patient populations such as Parkinson's disease and schizophrenia (Cools, 2006; Cools et al., 2010; Frank, 2005; Maia & Frank, 2017; Moustafa et al., 2008).

Method

The model is implemented using an updated version of the Leabra framework (O'Reilly, Munakata, Frank, Hazy, & Contributors, 2012), written in the Go programming language (see https://github.com/emer/emergent). All of the computational models, and the code to perform the analysis, are available and will be published on our github account. We first outline the basic neuronal framework before elaborating on the PBWM implementation, modifications to the continuous report task, and chunking implementation, with most details in the Supplementary materials.

Leabra uses point neurons with excitatory, inhibitory, and leak conductances contributing to an integrated membrane potential, which is then thresholded and transformed to produce a rate code output communicated to other units.

The membrane potential V_m is updated as a function of ionic conductances g with reversal (driving) potentials E according to the following differential equation:

$$C_m \frac{dV_m}{dt} = g_e(t)\bar{g}_e(E_e - V_m) +$$

$$g_i(t)\bar{g}_i(E_i - V_m) + \\ g_l(t)\bar{g}_l(E_l - V_m), \tag{1}$$

where C_m is the membrane capacitance and determines the time constant with which the voltage can change, and subscripts e, l and i refer to excitatory, leak, and inhibitory channels respectively.

The excitatory net input/conductance $g_e(t)$ is computed as the proportion of open excitatory channels as a function of sending activations times the weight values:

$$g_e(t) = \langle x_i \rangle = n \sum_i x_i \tag{2}$$

Activation communicated to other cells (y_j) is a thresholded (Θ) sigmoidal function of the membrane potential with gain parameter γ:

$$y_j(t) = \left(1 + \gamma[g_e(t) - g_e^{\Theta},\right) \tag{3}$$

where g_e^{Θ} is the level of excitatory input conductance that would put the equilibrium membrane potential right at the firing threshold Θ and depends on the level of inhibition and leak.

$$g_e^{\Theta} = \frac{g_i(E_i - \Theta) + g_l(E_l - \Theta)}{\Theta - E_e}$$

Further details are in the supplementary material, but we elaborate the inhibition calculation below as it becomes relevant for the chunking mechanism.

Base PBWM model

The PBWM model is built based on a large repertoire of research surrounding WM, gating, and RL and has been developed over a series of articles (see introduction). Here we focus on the high level description of its functionality and the unique additions to the current application, particularly the implementation of continuous rather than discrete representations throughout the network (input, PFC and response layers), and the chunking mechanism.

We modified PBWM to accommodate continuous representations such as those used in the delayed report color wheel task (Berg et al., 2012; Nassar et al., 2018), see Figure 1a, a common task to assess precision and recall characteristics of VWM and which forms the main basis for our simulations. In this task, participants are presented with multiple colored bars on a visual display where each bar has two attributes: a color and orientation. After some delay, participants are shown only one of the orientations in gray, and the subject's task is to report the color that was associated with that orientation using a continuous color wheel. Previous PBWM applications used only discrete stimuli and did not address precision. To simulate continuous report tasks, we represented the color for each stimulus as randomly varying from 0 to 2pi using a population code, where each neuron in the layer maximally responds for a particular color, and the full representation for a given continuous input is represented as a Gaussian bump over an average of 10 neurons in a 20 neuron layer. This representation accords with that seen in visual area V2, with hue neurons that are spatially organized according to color (Xiao, Wang, & Felleman, 2003). Each color was presented to the network together with a separate representation of its associated orientation (for simplicity we used discrete orientations, as the task is not to recall the precise orientation but only to use it to probe the color). The stimuli are presented sequentially to the mode. This serves 3 purposes: to simplify the binding problem, to mimic a sequential attentional mechanism, and to make contact with literature on serial WM tasks.[1].

These input layers project to the PFC maintenance layers, which contain isolated populations in discrete stripes, also coded as Gaussian bumps of activity. As in prior PBWM models, the PFC is divided into superficial and deep layers (Frank & Badre, 2012; Hazy et al., 2007; Hazy, Frank, & O'Reilly, 2021; O'Reilly & Frank, 2006). The superficial PFC layers for each stripe will always reflect the input stimuli transiently, as candidates to be considered for storage in WM. But for these stimuli to be maintained robustly over delays (and over intervening other stimuli on subsequent time points), they have to be gated into WM. Accordingly, each PFC stripe is modulated by a corresponding BG module consisting of striatal "Go" and "NoGo" units which in turn, via direct and indirect pathways, project to BG output / thalamic units. When there is relatively more Go than NoGo activity in a given module, the corresponding Thalamic output unit

[1]While this sequential presentation of stimuli simplifies the binding problem, it also adds a further challenge as the network must have capacity to recall items that were presented several time steps/trials ago. To solve this problem, the model must learn an efficient and appropriate gating strategy. This also makes the model vulnerable to serial dependence it its chunking, consistent with that observed empirically, whereby WM reports are biased towards the last stimulus that was presented Bliss, Sun, and D'Esposito (2017); Fischer and Whitney (2014); Kiyonaga, Scimeca, Bliss, and Whitney (2017)

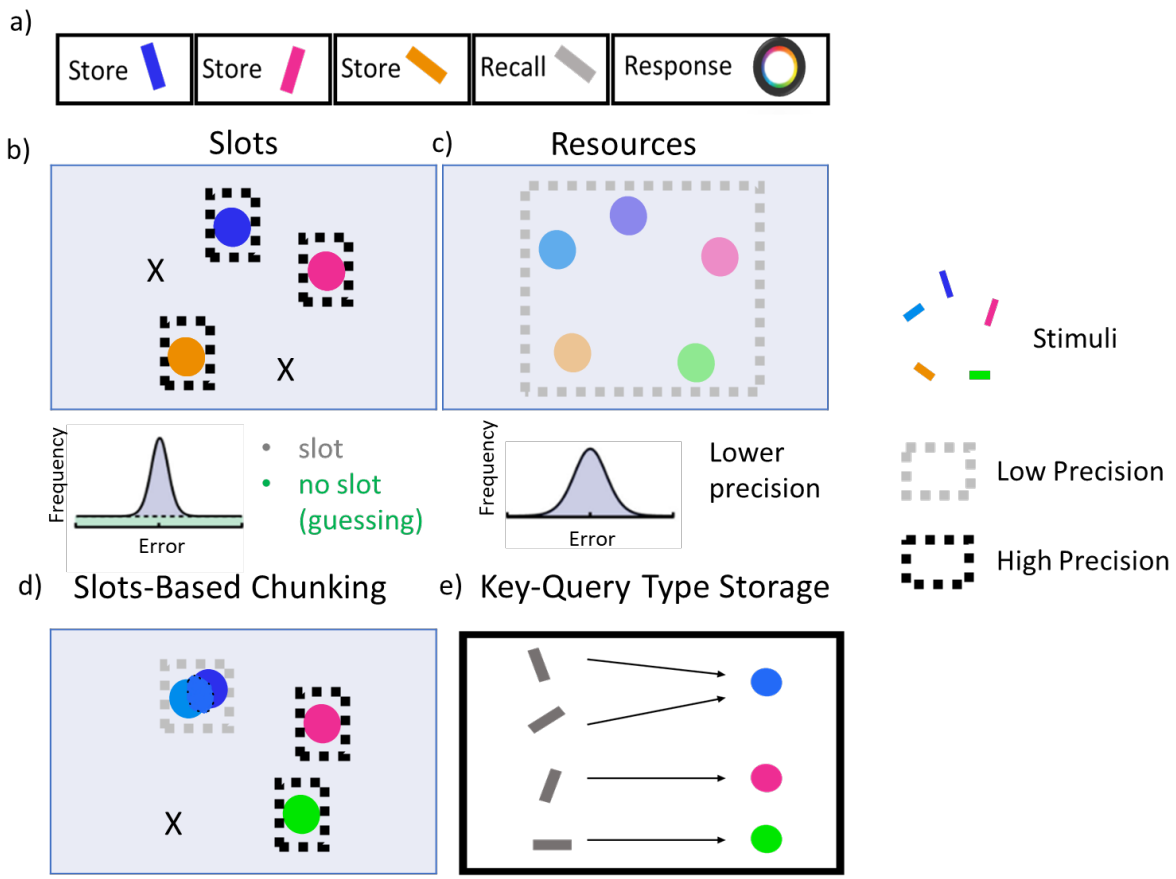

Fig. 1 Visual Working Memory Task. a) The color wheel task is commonly used to study the nature of capacity limitations in VWM. During encoding, participants are presented multiple randomly generated oriented and colored bars. After a delay they are shown a recall probe trial in which one of the previously seen orientations is presented in gray. The participant responds by using a color wheel in an attempt to reproduce the color associated with that probe orientation. The number of store items are dictated by **set size**. b) Slots models suggest that WM capacity is limited by a fixed number of slots. When set size exceeds capacity, some items are stored in memory with high precision while the rest are forgotten, resulting in an error histogram that is a mixture of high precision memory (for items in a slot) and guessing (for items not in a slot). c) Resource models state that all items can be stored in a common pool, but as the number of items increase, the precision of each representation decreases, resulting in an error histogram with a large variance (but no guessing). Adapted from (Ma et al., 2014). d) A hybrid chunking model containing discrete slots, but with resource-like constraints within each slot. Here, the two bluish items are merged together within a slot, reducing their precision but freeing up other slots to represent pink and green items with high precision. The orange item is forgotten. The criterion for chunking can be adapted such that error histograms will look more like the slots theory or resource theory depending on task demands (WM load and chunkability of the stimulus array; (Nassar et al., 2018)). e) Storage in the PBWM-chunk model is like a key-query. The colors are stored as continuous representations in PFC and can be merged. The orientations are the queries used to probe where information should be stored and where to read it out from.

is activated, inducing thalamocortical reverberation and activation of intrinsic ionic maintenance currents, thereby triggering robust maintenance of information in the deep PFC maintenance layers (Frank & Badre, 2012; Hazy et al., 2007, 2021; O'Reilly & Frank, 2006). Thus only the stripes that have been input gated continue to maintain the most recent color representation in an attractor over time. Importantly, gating in PBWM implements a form of "role-addressable" memory: the decisions about whether and which stripe to gate colors into depends on its assigned role. In this case, the orientation probe associated with the color determines where it should be gated. By receiving inputs from the orientations, the BG can thus learn a gating policy whereby it consistently stores some orientations into a particular PFC stripe, making it accessible for read out. Figure 2 shows a schematic example in which, based on the orientation the network gates the first PFC stripe to store the green color, but then stores the color of the second orientation to store the red color. Thus, the PBWM stripes serve a variable binding function (O'Reilly & Frank, 2006) which can also be linked to key/query coding (Traylor, Merullo, Frank, and Pavlick (2024) see also Swan and Wyble (2014)); in this case the network can learn to use the orientations to guide which stripe is accessed, and the population within the stripe represents the content (color).

During a recall trial, the network is presented with only a single orientation probe. The model needs to correctly "output gate": select from multiple PFC maintenance stripes, so that only a single representation is activated in the corresponding PFC "output stripes", which in turn projects to the output layer (Figure 2 bottom row). If it correctly recalls the associated color (by activating the color population in the output

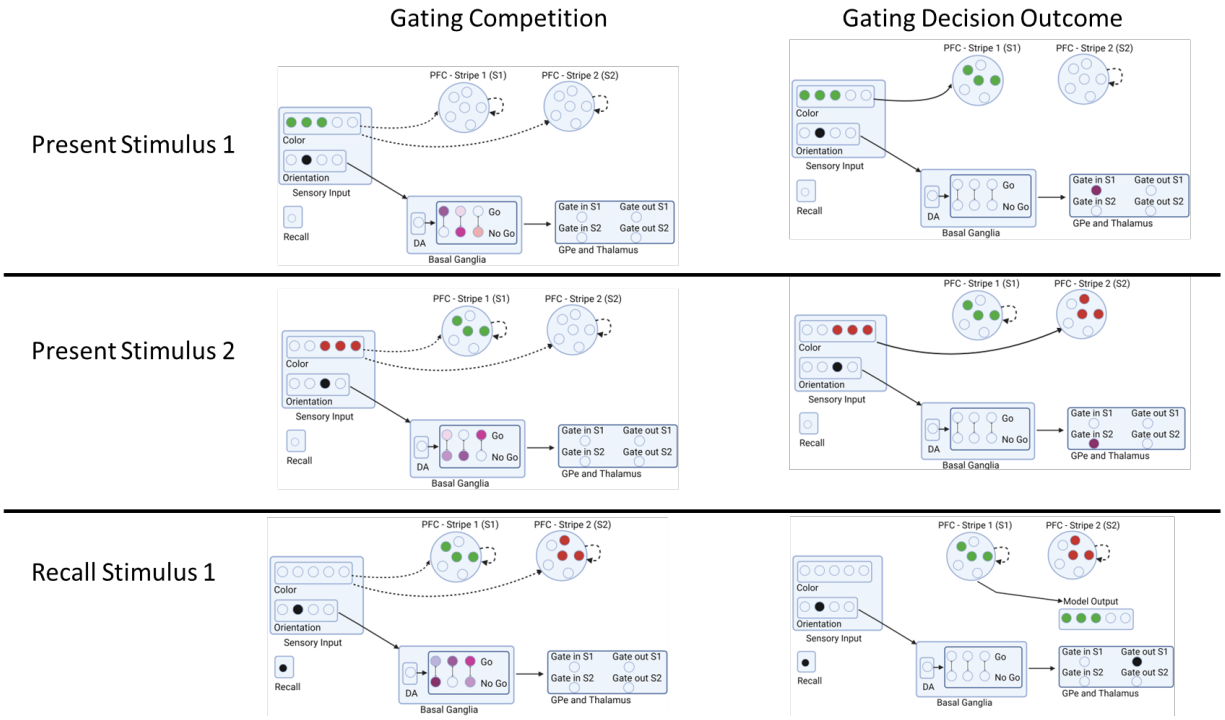

Fig. 2 Example Sequence of Network Gating Decisions. In this example trial, the network is presented with stimulus 1 (color and orientation), stimulus 2, and is then asked to recall the color of stimulus 1 based on just its orientation. Each step is broken into a gating competition that involves the Basal Ganglia (striatal Go/NoGo units, Gpe/Gpi) and Thalamus units. The outcome of this internal competition determines the gating decision and the model output. When the first stimulus is presented, the relative activities determine if and where the stimulus is gated in (stripe 1 or stripe 2). The network gates stimulus 2 in a different stripe based on its orientation. During recall, the network uses a gating policy to output gate the stripe corresponding to the probed orientation. A reward is delivered to the network proportional to the accuracy in reporting the original color. A negative reward is delivered if the color is not sufficiently close (see Methods). Rewards translate into dopaminergic reward prediction error signals that serve to reinforce or punish recent gating operations. This schematic is illustrative; the actual network contains a broader population code and the PFC stripes are divided into input and output representations, each with deep and superficial layers (see Text).

layer) it receives a reward. Rewards were given in a continuously linear fashion based on the difference between output and the target color. The activity of the output neurons was decoded (using a weighted linear combination of neuron activities; (Almeida et al., 2015)) and the reward given was inversely proportional with the error. Correctly recalling a color thus requires not only having it stored in PFC, but reading out from the correct stripe that corresponds to the probed item. This read-out operation involves a BG output gating function (Frank & Badre, 2012; Hazy et al., 2007; Kriete et al., 2013), facilitating transmission of information from a PFC maintenance stripe to the corresponding PFC output stripe. In this way, the model can read out from its several stored WM representations according to the current task demands (see (Chatham et al., 2014) for neuroimaging evidence of this BG output gating function). The input and output gating mechanism in PBWM performs a role-addressable gating function that can be linked to the key-query operations in Transformers ((Traylor et al., 2024)).

Note that successful performance in this and other WM tasks (Frank & Badre, 2012; Hazy et al., 2007) requires learning both the proper input gating strategies (which PFC stripes to gate information into, depending on the orientation, and which to continue to maintain during intervening items), and output gating strategies (which PFC stripes to read out from in response to a particular orientation probe). Such learning is acquired via reinforcement learning mediated by dopaminergic signals projecting to the striatum (represented by the bottom half of the model). At the time of recall, the network receives a dopamine (DA) burst or dip conveying a reward prediction error signal (RPE, by comparing the reward it receives with the reward it expected to receive using a Rescorla Wagner delta rule algorithm). These DA signals are used to modulate synaptic plasticity in the Go and NoGo units, reinforcing corticostriatal Go signals that drive adaptive input and output gating operations (following positive RPEs), and reinforcing NoGo units that suppress ineffective gating strategies (following negative RPEs). (See Supplement for information on parameter searching for other parameters of the model.)

Chunking / nearest neighbor implementation

This model was augmented with a chunking layer. This layer represents posterior cortical association areas that receive strong excitatory input from both sensory regions and (weaker) top-down information from deep PFC maintenance layers (Figure 3a). This connectivity ensures that the chunked layer will primarily respond to the input, but that if any of the currently maintained PFC representations is close enough to that input, the overlapping neural activations will be enhanced, thereby biasing the Gaussian bump to reflect the combination of the input and the nearest PFC representation(s). Lateral inhibition within the chunk layer ensures that only the most excited units will remain active. As such, the chunk layer will either represent the original incoming stimulus (if no PFC representation is sufficiently close to it) or a combined representation between the incoming and existing stimuli (Figure 3b).

The excitatory conductance to the chunking layer comes from both the input layer and the PFC and can be summarized in the following equation:

$$g_e(t) = \frac{1}{n} \sum_i x_i w_i \tag{4}$$

where $g_e(t)$ is the excitatory conductance (input) to a layer, x_i is the activity of a particular sending neuron indexed by the subscript i, w_i is the synaptic weight strength that connects sending neuron i to the receiving neuron, and n is the total number of channels of that type (in this case, excitatory) across all synaptic inputs to the cell. Note that the relative strength of projections from input to PFC is scaled with larger influences of input than PFC (to reflect e.g., number of synapses or proximity to the soma, using a relative weight scale (w_i) (see supplement andRandy O'Reilly (2020) Chapter 2 for detailed information). This allows the chunking layer to preferentially reflect the input, subject to an attraction toward PFC representations that overlap with it (the nearest neighbor; Figure **??**).

Lateral inhibition regulates the amount of activity in the chunking layer and determines how close representations must be to result in either chunking or the original stimulus being represented in the chunk layer. Lateral inhibition is implemented using feedforward (FF) and feedback (FB) inhibition (FFFB) which both alter the inhibitory conductance $g_i(t)$:

$$g_i(t) = \mathrm{Gi}\,[\mathrm{ff}(t) + \mathrm{fb}(t)] \tag{5}$$

,

where feedbforward inhibition ($ff(t)$) is determined by the summed net input to the layer and feedback inhibition ($fb(t)$) is determined by the firing rates of the neurons in that layer, and the Gi gain parameter determines the overall sparsity of the layer (i.e., the relative influence of inhibition compared to excitation Ge).

Critically, different stripes within PBWM receive projections from either the original sensory input or the chunking layer. As such, PBWM could learn a gating strategy to store either the original sensory input into PFC (as in the base model) or to store the chunked representation into one of its PFC stripes. In the latter case, it would replace the previous item stored in the corresponding PFC stripe with the new chunked representation, incorporating the novel input stimulus. These gating strategies are not hard-wired but are learned. For instance, the network could learn to use a certain stripe for some of the orientations and use the other stripe for the rest of the orientations, allowing it to appropriately manage where to store and read out from according to the probe, with precise memory for those representations that are stored and accessed. At the other extreme, the model could also learn to preferentially gate representations into and out of the chunk stripe. We will see later how the model gating policy depends on task demands (specifically set size) and evolves with learning.

For each experiment, at least 80 separate random seeds were run for each condition: chunk and no chunk. For some select analyses requiring more observations, 160 separate random seeds were used for each condition. Results are based on averages across those models. To test how set size affects learning and recall, the models are trained and tested with set sizes 2, 3, or 4. The set size determines the maximum number of stimuli that can be presented before recall trials. Set size 2 means that all trials have 1 or 2 items. Set size 4 means that networks have to maintain up to 4 items before receiving a recall probe, and it may have to recall any of the preceding items.

Results

We focus our simulations on variants of the color wheel task (see Methods). Briefly, networks are presented with continuous sensory inputs represented as coarse-coded Gaussian bumps of neural activity in conjunction with their associated discrete orientation. The number of stimuli to store ("set size") before a recall trial varied between 2 and 4 items. During recall, a single orientation was presented to the network and it had to reproduce the associated color in the output layer.

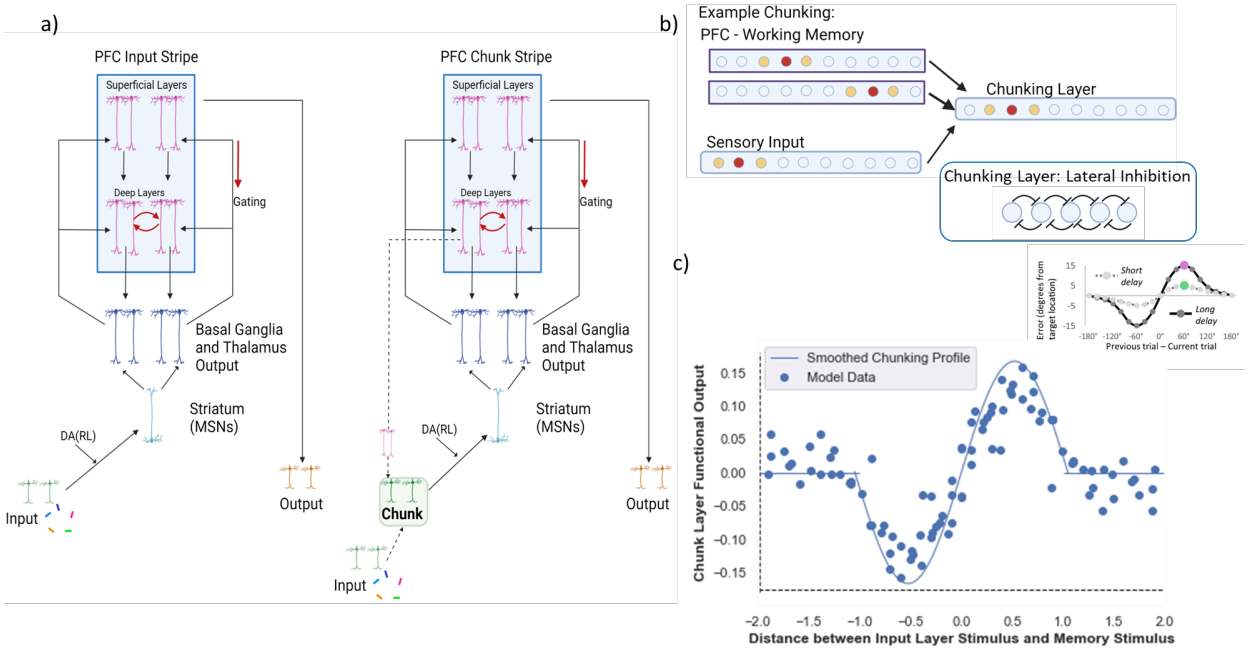

Fig. 3 PBWM Model and Chunking Layer Details. a) Network diagram in the case of two stripes: the first PFC stripe receives projections from the input layer ("PFC Input Stripe); the second PFC stripe receives projections from the chunk layer ("PFC Chunk Stripe"). The network can be scaled to include more stripes of either type. We will refer to this model as the "chunk model". The control model has two stripes that are both of the type "PFC Input Stripe" (but it can use them to store separate inputs). We will refer to this as the "no chunk model". b) Chunking schematic. A posterior chunking ring attractor layer receives inputs from two PFC stripes (maintaining separate stimuli/representations) along with the sensory input. Overlap between the sensory input and the first PFC representation leads to convergent excitatory input in the chunking layer, resulting in a merged attractor. The impact of the more distant PFC representation is suppressed due to lateral inhibition. c) Chunking profile based on similarity. The x axis shows the difference between the incoming stimulus and the existing (one) stimulus in the WM layer. The y axis how far the representation in the chunking layer deviates from the input stimulus. If the difference has a small magnitude, the input representation stored in the chunking layer is attracted toward that in the PFC WM layer. Once the difference between the input stimulus and the stimulus stored in the PFC layer is too large, the chunking layer largely mirrors the input (due to stronger input than PFC projections). This chunking profile closely matches that seen human memory representations, whereby memory reports are biased toward recent stimuli (top right inset, adapted from (Kiyonaga et al., 2017)).

During a recall "probe" trial, only an orientation is input to the model, with no color (as in the empirical versions of this task). The model outputs a continuous population-coded response that can be decoded as a specific color; the error is then simply the difference between this decoded output and the ground truth value presented during the earlier store trial for that orientation. "Correct" responses show as data points when error is 0 degrees or close to 0 degrees. If the model outputs an incorrect color, but that color corresponds to a different orientation, this is referred to as a binding or swap error (Bays et al., 2009). Finally, if the response is incorrect and nowhere near any of the colors for the stored orientations, it would be referred to as a guess. A guess could land anywhere along the axis of -180 to 180 degrees and as such manifests as a uniform distribution across trials. If the model produced a non-response (nothing was gated out, e.g. if a stripe was empty), we randomly sampled from the uniform distribution ((Almeida et al., 2015) followed a similar process), mimicking random guessing. These errors (correct responses, guesses, binding errors) manifest themselves in the error distribution.

For proof of concept, we chose to use a minimal set-up in which all models were allocated 2 PFC maintenance stripes (we relax this assumption later to compare to models with larger allocated capacity). For all simulations, we compare performance (error distributions, gating strategies, influence of dopamine manipulations) between networks with chunking ability (the "chunk model") against those with equivalent (or larger) number of stripes. We refer to the "allocated capacity" as the number of stripes given to the no-chunk model, because this is a hard limit on the maximum number of representations that can be stored and accessed. We refer to the "effective capacity as the potentially larger number of items that can be accessed due to an efficient gating policy. Effective capacity can be improved if the network learns to consistently store (input gate) colors of distinct orientations in distinct stripes, and to appropriately read out from (output gate) the corresponding stripe at recall trial. It can also potentially be improved via chunking by increasing the number of representations that can be stored and accessed.[2]. It is thus important to note that

[2]Note however, that effective capacity is not always larger than allocated capacity: without learning an effective input and output gating policy, a network's effective capacity will be less than its allocated capacity, for example if it overwrites information in the same stripe, if it accesses the incorrect stripe during recall, or if it doesn't gate a stimulus at all

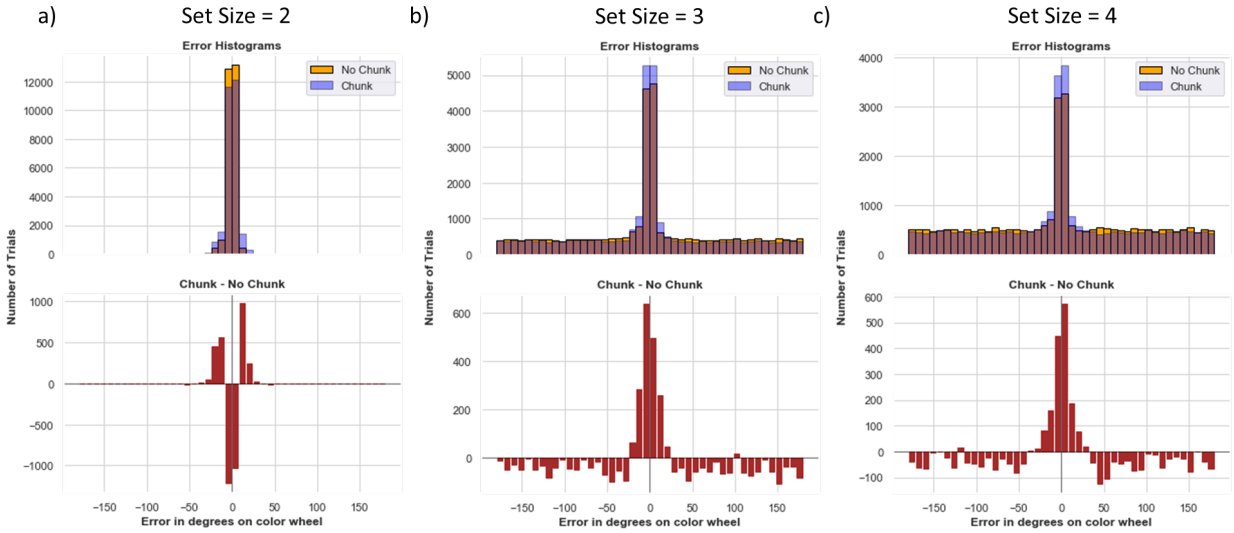

Fig. 4 Model Recall Error Histograms. The error in degrees is plotted on the x axis, the number of trials on the y axis. The blue and orange histograms show errors from all recall trials across all 80 weight initializations from the chunk and no chunk models, each allocated with two stripes. The red histogram plots a bin-by-bin difference in errors between the models. a) For set size 2, there is very little difference between the models. The chunk model exhibits slightly higher rates of low errors neighboring zero (up to 30 degrees), due to small losses in precision resulting from some chunking (because this network has only 2 stripes, both input and chunk stripe must be used to maintain and access both stimuli). b) Set size 3 is beyond the number of stripes allotted to the network. The chunk model has a larger density at zero and small errors, and less guessing (reduced density in the uniform distribution, see red lines). c) At set size 4, the chunking advantage is manifest by low errors and the improvement in less guessing becomes more pronounced (note y-axis scale - the reduction in guessing is actually reduced for set size 4 compared to 3).

improving effective capacity requires an effective learning process to develop adaptive gating strategies, as the networks are not hard-coded to use any stripe for storing or accessing any representation. We will show how such learning depends on a healthy balance of dopaminergic RL signals in the basal ganglia.

Error distributions across set sizes mirror those in human VWM and show chunking advantages

Figure 4 shows a histogram of network errors (in degrees) during recall trials. The comparisons are made between chunk and no-chunk models as well as set sizes 2, 3, and 4; in these simulations we begin with a minimal setup in which both networks are endowed with two stripes. When set size is equal to the number of stripes (2), errors are small and centered around 0, with some variance due to precision. The overall performance is similar between models, but note that the chunk model shows somewhat more imprecise responses as indicated by some more small error trials. The ability to chunk results in a small cost which manifests as a decrease in precision when chunking occurred but did not need to be used.[3].

As set size increases beyond the allocated capacity, both models resort to guessing (random errors) on a subset of trials. This pattern is observable by the error histogram containing a mixture of errors centered around zero and a uniform distribution (see Figure 1), as commonly observed in humans (W. Zhang & Luck, 2008). Notably, the chunking model guesses less than the no chunk model and has a higher chance of precisely recalling the items (Fig 4). The difference between the chunk and no chunk model widens as the item limit continues to grow beyond the number of stripes. Comparing chunking and non-chunking models illustrates how the benefit of chunking is task-dependent. We next explored how chunking may improve the effective capacity of the network beyond the allocated number of stripes, and more specifically in which trials the advantage manifests, motivated by similar analysis in humans (Nassar et al., 2018). We subsequently explore how these strategies are acquired via reinforcement learning.

Chunking Frees Up Space for Other Items

A key normative motivation for chunking is that doing so can save space to store other items, thereby improving effective capacity (Nassar et al., 2018). In the model, when two items are chunked into one stripe, the second stripe is free to hold another item. One key prediction is that chunking should not only manifest

[3]Note that the chunk model is endowed with two stripes, and thus the only way for it to recall both items is to use both the input stripe and the chunk stripe. As a result, at least one item could be stored precisely in the input stripe, but if the other item is close enough to it for the chunk layer to merge the two, the PFC will store the less precise chunked representation in the chunk stripe, and memory reports will be biased. The network can nevertheless store two precise items if they are far enough apart such that the chunk layer is not biased by the other PFC representation (see Figure 3)

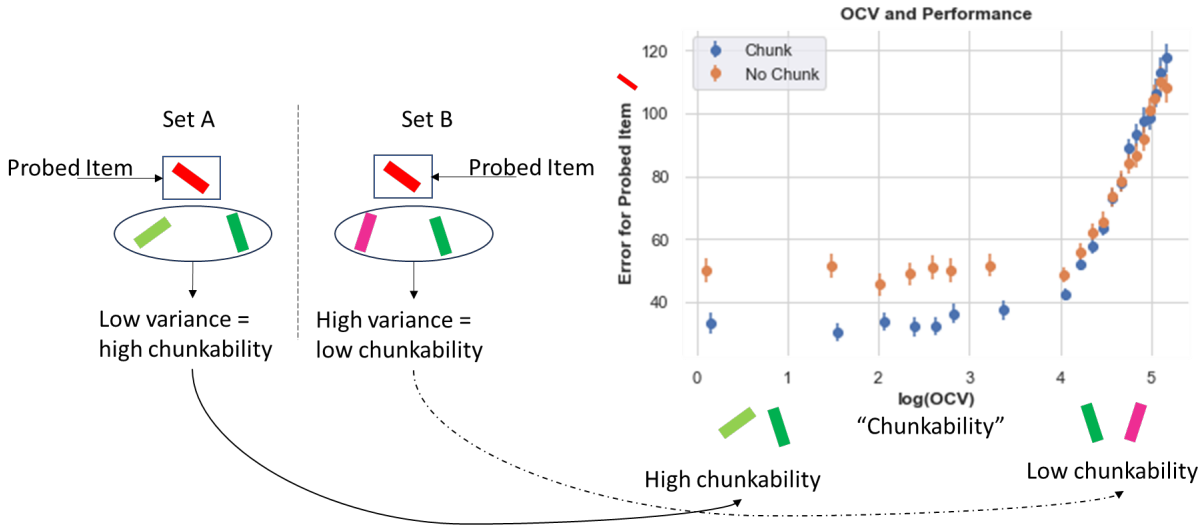

Fig. 5 Chunking improves recall for non-chunked items. Left. Example array. Here we compare 2 sets, both containing a red item that will be later probed. In Set A, the other items (out of the probed cluster) are two shades of green and thus low variance (are similar to each other) and are therefore more likely to be chunked. In set B, the out of cluster variance (OCV) for the green and pink items is higher and these items are not likely to be chunked. Right. Chunking networks show consistent Recall advantages (lower errors) when OCV is low and hence the other items are chunkable. This difference disappears as OCV increases and overall errors rise. Errors plotted over all trials averaged over 80 networks in each case.

in terms of loss of precision when probed with any of the chunked items, but improved memory for the other items (Figure 1). Consider the situation in Figure 5 left, for a set size of 3. In both Set A and Set B¸ the red item is the probed item (the one that the model is asked to recall). Set A contains other items in the set that are different shades of green (low variance) and thus "chunkable". If the network chunks them together, they will occupy one stripe and the second stripe will be free for the red item, which is then more likely to be recalled at high precision (as it is not part of the chunk). In Set B, the other items are pink and green and are thus not chunkable (high variance). The network may store each of these into a separate stripe, forcing it to randomly guess when probed with the red stimulus. (Alternatively, the red item could be chunked with the pink item, in which case it will be recalled but with less precision than if it stored only the original red item). To formalize and test this intuition, we quantified the "out of cluster variance" (OCV) as the variance in degrees between the "other" items in the set (i.e., the items that are not probed) across all trials (See Supplement for details on OCV calculation). When this variance is low, those items are more chunkable. We then assessed whether accuracy on recalling the probed item (not part of this chunk) is improved as a proxy for chunking behavior.

Indeed, the data supports this prediction (Figure 5). When other items in a set are chunkable (low OCV), the chunking network exhibits significantly smaller errors than the control network on the probed item. After some OCV threshold, the chunking network no longer exhibits an advantage, and both networks show increasing errors. (The increasing errors likely result from "swap errors" (Bays et al., 2009), i.e., when the network reports one of the other stimuli in its memory instead of the probed item - this results in larger errors as the entire set is more uniformly spaced and thus not chunkable.) In sum, this analysis confirms that chunking does not merely result in reporting less precise responses for nearby items due to perceptual similarity, but that the network leverages such similarity to its advantage so that it can save space for storing and recalling other items, as also seen in humans (Nassar et al., 2018).

Chunking leads to better resource management

In addition to overall better performance, we hypothesized that networks that can chunk can manage memory resources more efficiently than the no-chunk control models. We next compare how the models use the allocated resources, focusing on store trials in which the number of stimuli equaled the set size (e.g., 4 items stimuli were always present for set size 4). We also first focus on the performance of networks after learning; below we explore how the chunk network learns to use the different gating strategies over the course of learning for different set sizes.

When the set size is 2, after learning, chunk and no-chunk models are equally able to utilize both stripes on 100% of the trials (Figure 6). The networks can properly gate both colors into distinct memory slots without overwriting or reusing the same stripe (in which case Fig 6 would have shown reduced use of one or the other stripe).

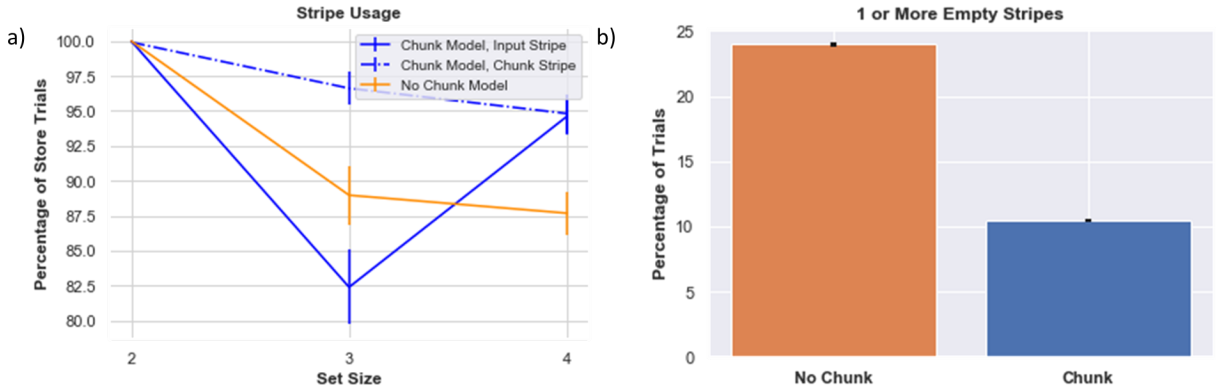

Fig. 6 Stripe Usage a) Stripe usage for the 1) chunk model, chunk -linked stripe 2) chunk model, input-linked stripe 3) no chunk model (average across both stripes), b) Proportion of trials when at least one stripe was empty. This analysis was done over 160 different model initializations.

As the set size increases beyond allocated capacity, the gating management problem becomes much harder to solve via RL, and overall performance declines, particularly in the no-chunk (control) model. Indeed, one might expect that as the number of items are increased, the model should always "max out" the number of stripes used, but in fact the opposite is the case. When the network attempts to gate information into both stripes, the no-chunk model will often receive negative reward prediction errors during recall trials when it will inevitably be forced to guess for a subset of the stimuli that is not in its allocated memory. As a result, input gating strategies will be punished, even if they were successfully employed and would have been useful had the other stimuli been probed. In turn, due to punishing gating policies that are generally useful, the stripe usage actually decreases, and the stripes are sometimes empty, akin to "giving up". Conversely, if the network happened to be positively reinforced for gating a particular stripe, it might promiscuously gate that same stripe. This leads to overwriting information even though the other stripe is empty, and forcing the network to guess (or emit a non-response) when probed with a stimulus that was overwritten. In sum, the model is exhibiting a non-monotonic use of its resource, as its effective capacity actually declines relative to its allocated capacity. This result is reminiscent of experimental data in fMRI and EEG showing that PFC activity increases with increasing set size but then plummets when set size exceeds the participants capacity (e.g. (Jaeggi et al., 2003; D. Zhang, Zhao, Bai, & Tian, 2016)), perhaps indicating a "giving up" strategy. We will explore the dopaminergic RL basis of such giving up in a section below.

In contrast, the chunk model is more effective at managing its resources when set size exceeds allocated capacity (Figure 6). Recall that the chunk model has access to one stripe linked to the chunked representation ("chunk stripe") and one stripe linked to the original input representation ("input stripe"). As set size increases, the network has more opportunities for chunking, and accordingly, relatively more instances of reinforcing the gating operation linked to the chunk stripe. Interestingly, as set size just exceeds allocated capacity (here, for set size 3), the network decreases its use of the input stripe. This pattern arises because the network learns an advantage of chunking for set size 3 and thus sometimes does so more than it needs to (freeing up the input stripe), but also because of the cost of relying too much on the input stripe (as per the no-chunk model). Finally, as set size increases further (set size 4), the chunk network learns the benefit of storing some items in the held out input stripe, increasing effective capacity, while still effectively using the chunk stripe.

In sum, this analysis suggests that resource management and utilization is more consequential than the absolute number of stripes available. In previous network models of visual WM (Almeida et al., 2015; Edin et al., 2009; Nassar et al., 2018; Wei et al., 2012), responses were considered "correct" if the probed item was stored somewhere within the network; i.e., networks were not required to select among these stored representations in response to a probe, and they also did not have to decide whether or not to store an item in the first place. In contrast, the PBWM model focuses on the control of gating strategies into and out of WM, but requires RL to do so. Errors can result from reading out the wrong stripe (a swap error) or from an empty stripe (leading to guessing or non-responding). Chunking is an information compression mechanism that allows multiple stimuli to be mapped onto the same stripe. The chunk stripe has the advantage of being used repeatedly, giving the network has more opportunities to learn how and when to use that stripe.

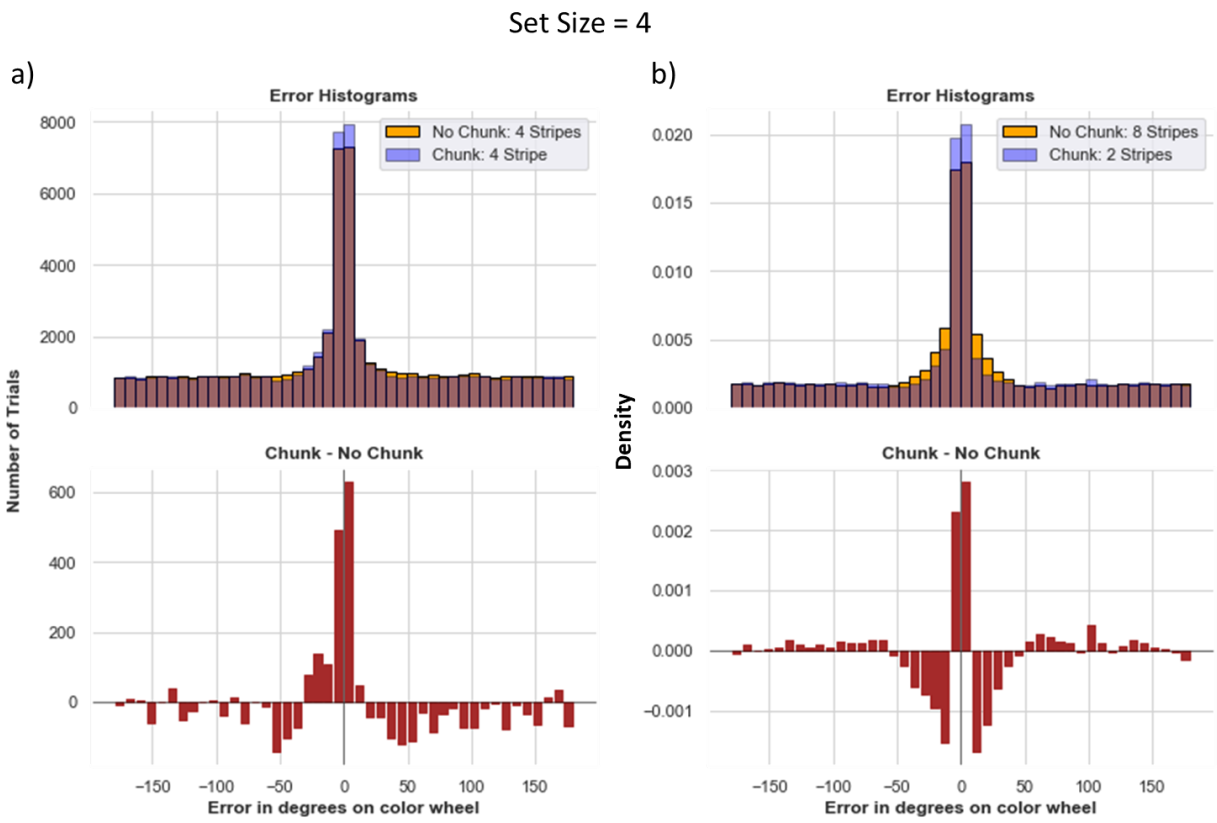

Fig. 7 Increasing Allocated Capacity ≠ Better Performance: The importance of Resource Management a) Chunk Model with 4 stripes vs. No chunk Model with 4 stripes in a task with set size 4. Even though the no-chunk networks has sufficient number of stripes to store each item with high precision, the corresponding chunk network still exhibits advantages, due to difficulties in credit assignment associated with managing four independent stripes. b) A more extreme comparison between the Chunk Model with 2 stripes vs. No chunk Model with 8 stripes. The chunk model guesses slightly more, but has more precise responses. The 8 stripe model has more density at small nonzero errors (see text for explanation). For both a and b the averages were computed over 160 models. For b, we display density rather than counts, because trials where either models gave no response were removed to better understand the small nonzero errors in the 8 stripe model (nonresponses add noise).

Chunking advantages remain even when comparing to networks with higher allocated capacity

One might think that chunking advantages are limited to situations in which the allocated capacity is less than the set size. But when considering the challenges imposed in networks for which storage and access of items is not hard-wired, but must be learned, this is not a foregone conclusion. Indeed, above we saw that the number of stimuli stored by no-chunk networks was even lower than their allocated capacity, due to RL challenges. We reasoned that such challenges could persist even when allocated capacity is increased to include or exceed the set size, due to credit assignment challenges in networks that are required to learn gating strategies into and out of multiple independent PFC stripes.

We begin with an analysis of networks performing the most difficult task (set size 4) but now allocated 4 stripes (for both chunk and non-chunk networks; in this case the chunk network has just one chunk stripe and 3 input stripes). The naïve hypothesis states that no-chunk and chunk models should not differ in performance, or that chunk models might even show a deficit due to loss of precision when using the chunk stripe. Instead, based on earlier results and the above, we reasoned that chunk models might continue to show an advantage here, because frequent reinforcement of gating into and out of the chunk stripe would reduce the credit assignment burden during learning that arises from learning to manage access of 4 different items into and out of WM.

Indeed, results supported these conclusions. Error distributions in chunk networks have more density at zero and low errors. The chunking model also guesses less (Figure 7).

This result largely persisted even in the more extreme case when allocating the control (no-chunk) model 8 stripes (twice as many as needed) and reverting the chunk model to using only 2 stripes. While guessing is slightly reduced when having more stripes (due to more opportunities to store stimuli), the 8 stripe model does not increase the number of times it precisely recalls the correct item relative to the chunk model with only 2 stripes (Figure 7b). Upon further inspection, one can see that the 8 stripe model produced a larger density of moderate errors around the 0-30 degree range. This result is curious because this model has no

ability to chunk. To disentangle the source of these errors and to lend insight into the difficulty of WM gating strategy with high load and/or allocated capacity, we first removed trials in which the network did not give any output (these non-responses comprised roughly 12% and 24% of trials from the 8-stripe model and the 2 stripe chunk model, respectively). Within the remaining trials, the 2-stripe chunk model has a higher peak of precise responses (around 0 error) but still slightly more guessing than the 8 stripe no-chunk model, which continues to show a higher density at moderate errors (0-30 degrees). The reason for these moderate errors is that with more stripes, the network has a more difficult job to reinforce output gating strategies that properly read out from only the most appropriate stripe, due to the curse of dimensionality (i.e., when the network outputs a response that is close enough to the target, it will get reinforced for any gating operations that preceded it, leading to spread of credit assignment to other stripes). Indeed, the over-extended 8 stripe network frequently reads out from (output gates) multiple stripes in parallel (an average of 2.53 stripes during recall), and thus when the response does reflect the correct item it is also "contaminated" by reading out on of the other stripes, such that the averaged response results in a larger number of moderate errors. In contrast, the two stripe networks (across both no chunk and chunk) output gated an average of 1.08 stripes for each trial, appropriately reading out from a single PFC representation.

In sum, simply allocating a network with larger numbers of stripes does not yield the naïve advantages one might expect, at least in the context of the need for gating strategies to be learned rather than hard-wired. In this case, the networks do use all the stripes available, but don't use them effectively. For example, a given network might gate one single stimulus into multiple stripes, and then proceed to overwrite many or all the same stripes with a new incoming stimulus – a strategy that is sometimes effective if it happens to get probed for the one of the items still in memory during recall. The large number of input and output gating operations to consider in tandem needed for adaptive behavior leads to a vexing credit assignment problem, as it becomes a challenge to know which of several gating operations or several PFC representations are responsible for task success / error, and networks fall into an unfortunate local minimum. This credit assignment problem is mitigated by chunking, allowing the network to reinforce the same input and output gating policy across multiple instances.

Frontostriatal Chunking Gating Policy is Optimized via RL as a Function of Task Demands

The above results show that chunking networks confer advantages as set size grows, even compared to no-chunk networks that have a larger number of allocated stripes. Moreover, these advantages come with little cost when set sizes are lower (e.g., 2). To explore how the network can adaptively learn to chunk as a function of task demands, we quantified the evolution over learning of each network's "gating policy". Prior work has shown that PBWM develops a gating policy that predicts rapid improvement in task success when such policies mimic the task structure (e.g., for hierarchical tasks; (Frank and Badre (2012); see also Traylor et al. (2024) who showed that modern transformer neural networks mimic a PBWM gating policy when challenged with WM tasks). Here we assessed whether networks could adaptively learn a gating policy that prioritizes gating into chunk vs input stripes depending on task demands.

In PBWM and related networks, the gating policy is dictated by learned synaptic weights into striatal GABAergic medium spiny neurons (MSNs). These MSNs are classically divided into D1 "Go" MSNs and D2 "NoGo" MSNs, with opponency between these populations determining which actions are selected (i.e., those with the largest difference in Go vs NoGo activities; (Frank, 2005; Jaskir & Frank, 2023)). In the case of working memory, a network will be more likely to gate information into a particular stripe if the synaptic weights are larger for the Go in comparison to the NoGo neurons. The relative weights control the disinhibition of that particular stripe. When the network performs well and it gets a reward prediction error, dopaminergic signals modify plasticity into the corresponding D1 MSNs, reinforcing the gating policy that drove the cortical update. Conversely, errors associated with negative prediction errors lead to punishment of that gating policy by increasing synaptic weights into the D2 MSNs (Frank, 2005; O'Reilly & Frank, 2006). Below we confirm a key role for these dopaminergic signals in modulating adaptive performance. But first here we evaluated how they served to alter specific gating policies. We assessed PBWM gating policies in terms of the differences in Go vs NoGo synaptic weights for each stripe, and how they evolved over time when networks were trained for each set size. Specifically, we computed the summed synaptic connection strengths from the Control Input Units representing Store Orientations to the Go and NoGo input gating units in the PFC stripes corresponding to input or chunk:

$$GatingPolicy = \alpha_j = \left[\frac{\sum Go - \sum NoGo}{\sum Go + \sum NoGo}\right]_+ \tag{6}$$

(Here $[]_+$ indicates that only the positive part is taken; when there is less Go than NoGo, the net input to the Thalamus is 0).

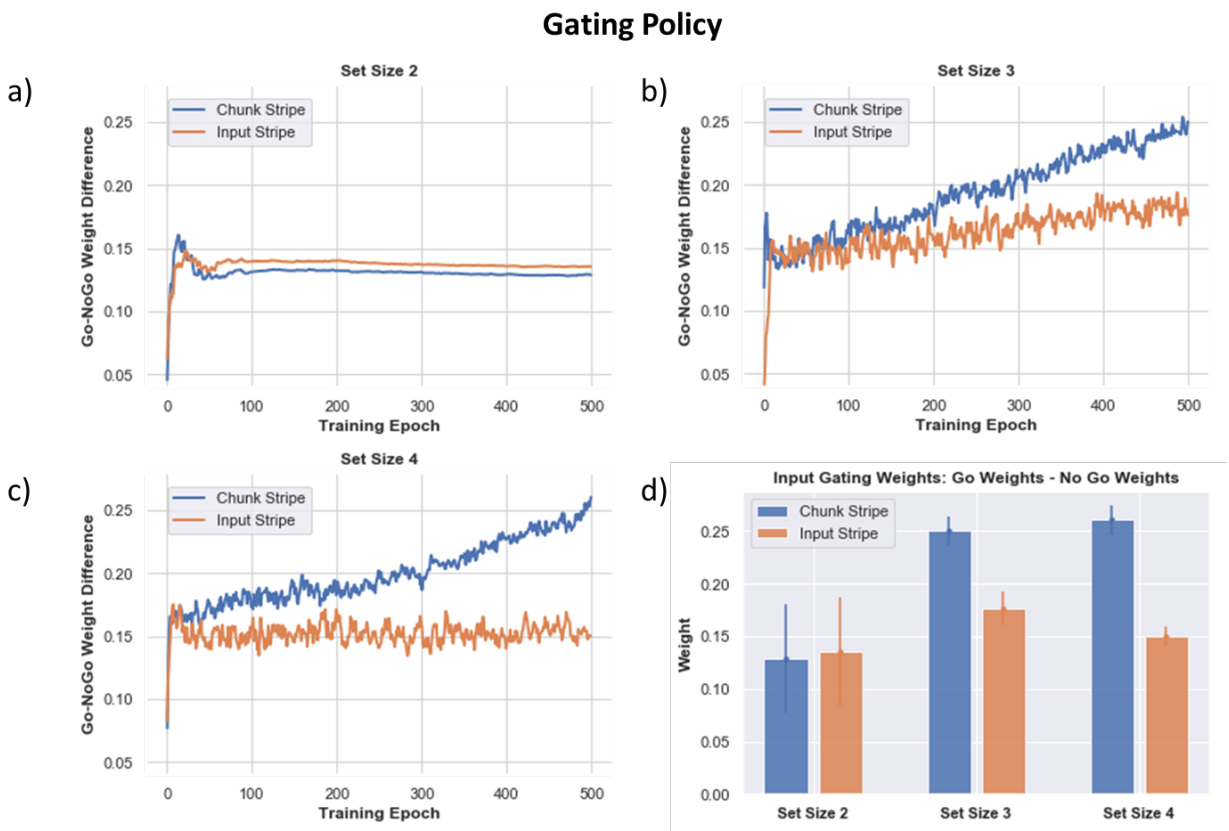

Fig. 8 Gating Policy (Go - NoGo Weights for Each PFC Stripe) Across Training As the networks learn (over 500 training epochs, averaged over 80 networks), the learned gating strategy differentiates between the input-linked (orange) or chunk-linked (blue) stripes. Positive values indicate the networks learn greater Go than NoGo weights for input gating stimuli into the corresponding stripe. a) Set size 2, the learned gating strategy shows a slight preference for the input stripe to be used (associated with increased precision), but the network also uses its chunk stripe in order to store the other stimulus (it is possible the chunk stripe stores a merged representation depending on the proximity of the stimuli) . b) As the set size increases to 3, the chunk stripe is increasingly preferred over training. c) This differentiation occurs earlier and more strongly for set size 4, where chunking has yet a larger advantage. d) Summary of Go - NoGo weights after training. A larger positive value shows a stronger preference for gating into that stripe. As set size increases, preference for gating into the chunk stripe increases.

If the network learns that gating information into the chunk stripe is useful, it will evolve stronger Go vs NoGo weights for that particular gating action. But if instead it is more useful to gate the veridical input stimulus, it will develop a stronger gating policy for that stripe.

Figure 8 shows how such gating policies evolve over time. At set size 2 - where allocated capacity (number of stripes) equals task demands, the gating policy slightly prefers to gate into the input stripe. This policy is sensible since the input stripe represents the original stimulus without any loss in precision, yielding lower errors. The network still learns a positive Go-NoGo gating policy for the chunk stripe, because it can use that to represent the other stimulus. Notably, as set size increases, the chunk stripe increasingly becomes the preferred stripe for input gating over the course of learning. This adaptive change in gating policy allows the model to optimize a tradeoff between recall quantity and precision with increasing WM load, mediating the performance advantages described above. These results also accord with those observed in humans by (Nassar et al., 2018)), whereby chunking propensities evolved adaptively as a function of reward history in their experiment, and also in their meta-analysis showing that chunking benefited performance more robustly in experiments with larger set sizes.

Dopamine Balance is Critical to Learning Optimized Gating Strategies; Implications for Patient Populations

As noted above, learning gating strategies in PBWM is dependent on the basal ganglia and dopaminergic reinforcement system. Both chunk and no-chunk networks must learn whether to gate items into WM, which stripes to gate them into so that they can be later accessed (leaving maintained information in other stripes unperturbed), and during recall, which stripe should be gated out (depending on the probed orientation). To learn this, the network uses a simple RL "critic" which computes reward expectations and deviations thereof in the form of reward prediction errors (RPEs). Positive RPEs are signaled by dopamine bursts which reinforce activity-dependent plasticity in striatal Go neurons corresponding to recent gating

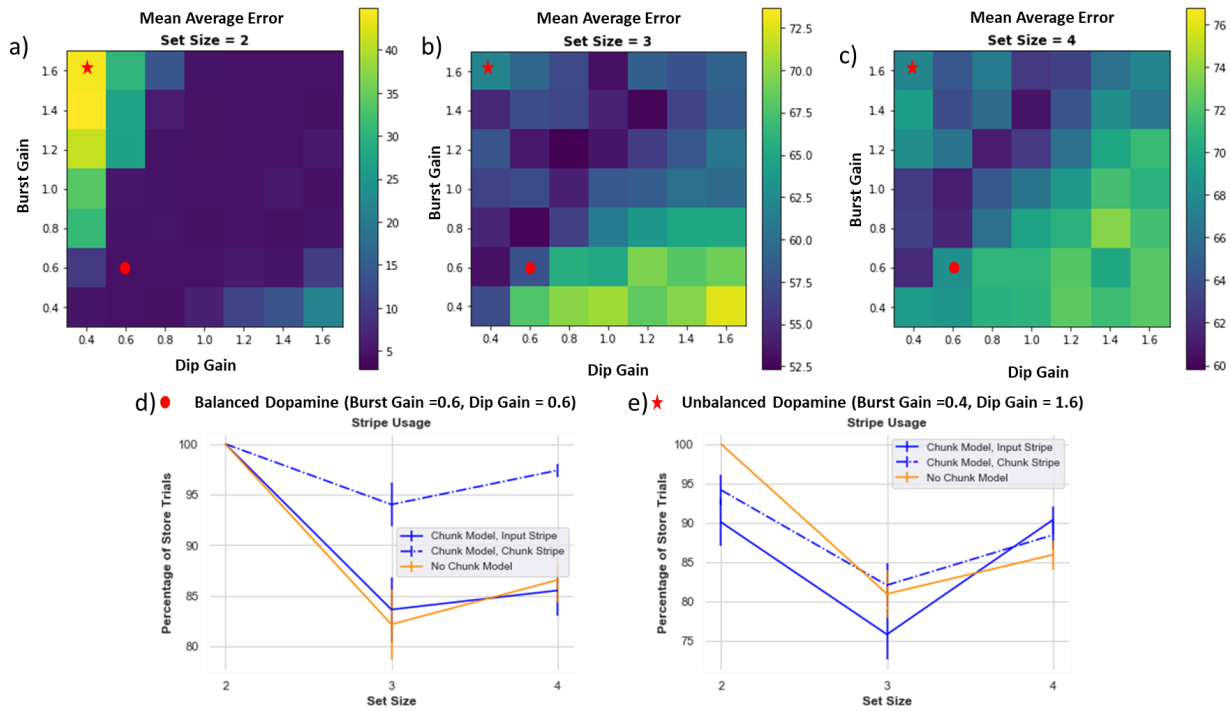

Fig. 9 Dynamic dopamine bursts and dips are needed for adaptive performance. Each box is an average absolute error over 80 models. The color bar on the right indicates performance (note different scales on each plot), with darker colors (blue) representing better performance / lower absolute error. a) Set size 2: best performance is across the axis where burst and dip gain are symmetrical. b and c) Set size 3 and 4: best performance is where burst gain is slightly higher than dip gain. d) Example of balanced DA (burst gain = dip gain = 0.6), stripe usage. The chunk model manages to use the chunk stripe across all set sizes and both stripes in set size 2. The no-chunk model shows diminished storage of both stripes with increased set size due to greater propensity of DA dips. e) A regime of DA imbalance (larger DA dip than gain). The chunk model fails to robustly use both of its stripes, losing its advantage. The RL parameters interact with the ability for the chunk model to properly leverage chunking.

operations (see Supplementary Materials and O'Reilly & Frank 2006 for details). Conversely, when the model receives a reward that is worse than expected (i.e., it reports an error), a dopamine dip (a decrease in phasic dopamine) will punish previous decisions. This negative RPE will punish the gating decisions by reinforcing corresponding NoGo neurons. To assess whether a healthy balance of such dopaminergic signals are needed for adaptive gating, we manipulated the gains of these dopaminergic bursts or dips to modulate their impact on Go and NoGo Learning. These investigations are relevant for assessing the basic mechanisms of the model but may also have implications for understanding well documented working memory impairments in patients with altered striatal dopaminergic signaling, such as Parkinson's disease, ADHD and schizophrenia (Cools, 2006; Cools, Gibbs, Miyakawa, Jagust, & D'Esposito, 2008; Cools et al., 2007; Maia & Frank, 2017).

Figure 9 shows how average absolute performance across 80 networks changes with DA burst and dip gain parameters. Overall a healthy balance of relatively symmetrical DA bursts and dips is needed for optimized performance, but this effect also interacts with set size. The best performance for set size 2 (Figure 9a) is along the axis where burst and dip gain are symmetrical. As set size increases, the task becomes harder, and rewards are sparser due to more errors. In this case the best performance is on the axis where burst gain is somewhat greater than the dip gain; the model learns best when it can emphasize learning from sparse rewards.

Dopamine reinforcement signals can also lead to "giving up" and diminish effective capacity. When set size increases, learning the proper gating strategies becomes difficult. The models may correctly gate a few items in, but they may be incorrectly overwritten or incorrectly output gated at time of recall. Importantly, incorrect responses generate negative RPEs that punish preceding gating actions, even if some of those actions were appropriate. A preponderance of negative RPEs can thus cause a network to "give up", as observed in the no-chunk models when set size exceeds allocated capacity, leading to empty stripes (Figure 6). This mechanism is conceptually related to rodent findings in the motor domain, whereby lower DA levels can induce aberrant NoGo learning even for adaptive actions, causing progressive impairments (Beeler et al., 2012).

Chunking can mitigate against giving up via shared credit assignment The chunk model can combat against using the "giving-up" strategy: when items are chunked, the chunk stripe is used more frequently and therefore has a greater chance of receiving the positive reinforcement, and thus benefits from shared

credit assignment. The model still has to learn when to use the chunk vs. input stripes, but chunking serves as an aid to the reinforcement learning process. Therefore, the chunk model is also more robust compared to the no-chunk model across various parameter ranges of dopamine. However, the chunk model still fails if the DA dip value is sufficiently larger than the DA burst, for similar "giving up" reasons (Figure 9 c,e).

Discussion

Our work synthesizes and reconciles theories of visual WM across multiple levels of abstraction. At the algorithmic level, there has been extensive debate regarding the nature of WM capacity limitations, with experimental results alternately supporting slots or resources theories (Bays et al., 2009; Berg et al., 2012; Swan & Wyble, 2014; Wei et al., 2012). At the mechanistic level, several studies across species and methods suggest that circuits linking frontal cortex with basal ganglia and thalamus support WM input and output gating (Baier et al., 2010; Chatham et al., 2014; Cools et al., 2010, 2007; McNab & Klingberg, 2008; Nakajima et al., 2019; Nyberg & Eriksson, 2016; Rikhye et al., 2018; **?**). These data accord with the PBWM and related neural network models of PFC-BG gating processes (Calderon, Verguts, & Frank, 2022; Frank et al., 2001; Hazy et al., 2007; Krueger & Dayan, 2009; O'Reilly & Frank, 2006; Stocco et al., 2010; **?**). To date, however, these lines of literature have for the most part not intersected. Here we show that when augmented with continuous population code values and a chunking layer, PBWM comprises a hybrid between slots and resources with resource-like constraints within individual stripes. Moreover, through reinforcement learning, adaptive gating policies can adjust the degree to which behavior mimics primarily slots-like or resource-like as a function task demands. As such, this model accounts for human findings supporting chunking of related items in WM, that such chunking evolves with reward feedback, and is predictive of better performance with increasing task demands across multiple datasets (Nassar et al., 2018).

On its surface, PBWM is ostensibly a slot-like model, with distinct PFC clusters ("stripes") corresponding to slots that can be independently gated, giving rise to useful computational properties such as variable binding, indirection, compositionality and hierarchical generalization (Kriete et al., 2013; O'Reilly & Frank, 2006; **?**). The need for gating also accords with data suggesting that effective WM capacity is related to management of WM content, ie. one's ability to filter out distractors so as to prioritize task-relevant information (Astle et al., 2014; Feldmann-Wüstefeld & Vogel, 2019; Vogel et al., 2005), and that such abilities rely on basal ganglia output and function (Baier et al., 2010; McNab & Klingberg, 2008). However, previous applications of PBWM and related networks have not confronted tasks requiring storage of continuous valued stimuli. In this work we augmented PBWM with a ring attractor layer that resembles that which has previously been applied to such continuous report tasks, supporting population level coding and mergers of nearby attractors (Edin et al., 2009; Nassar et al., 2018; Wei et al., 2012). However, in our network, this layer receives input from both the sensory input layer and from all the PFC stripes, and thus allows the network to combine sensory information with the nearest neighbor in memory. Moreover, WM chunking in our model is not obligatory, as the network can learn a gating policy that prioritizes raw sensory inputs (in which case it can represent a given item precisely) or to either replace a currently stored PFC item with the chunked version. As such, the PBWM-chunk model can learn to store more items than the allocated slots capacity by combining representations while incurring the cost of lost precision on the chunked items, giving rise to resource-like behavior. Given this learned policy, the network still may encounter trials where chunking is not possible and all stripes are occupied, leading to guessing and slots-like behavior. Depending on the learned gating policy and the task, the errors look more "slots-like" or "resource-like".

As such, our model addresses key limitations in previous neural models in this domain, in which chunking was obligatory fashion due to perceptual overlap and could not be optimized (Nassar et al., 2018; Wei et al., 2012). Instead, PBWM adapts whether or not to chunk as a function of task demands and reward history (Figure 8), similar to empirical data (Nassar et al., 2018). Further, PBWM can also report only the color of the probed item, unlike previous neural models which were considered accurate as long as the probed color was one of the various populations still active (Nassar et al., 2018; Wei et al., 2012).

Critically, to perform adequately, PBWM requires learning appropriate input and output gating policies which are not hard-wired, and indeed involves solving a difficult credit assignment problem (O'Reilly & Frank, 2006). At the input gating level, the network must learn whether to gate the chunked or the raw sensory stimulus (via updating of the chunk vs input stripe). Simultaneously it must also learn which stripe to output gate in response to a given probe, which requires coordinating its input and output gating strategies so that they align. The credit assignment problem, understanding which input gating decisions in combination with output gating decisions lead to reward, is difficult. To understand the difficulty, we can look at an example case where the model input gates into stripe 1. However, during read out, since it has not learned the proper binding yet, it gates out from stripe 2, leading to an error and a dopamine dip. In this case, due to an improper output gating decision, both input gating decisions and output gating decisions

will be punished. Eventual successful performance requires exploration of alternate gating strategies and reinforcement of those that are effective.

How can chunking help? First it is important to note that the above problem becomes even more difficult as the number of stripes increases – even if it matches or exceeds the set size (as shown in Figure 7). For example, random exploration and guessing will lead to the correct response (an item being gated into a stripe AND read out from the correct stripe) 50% of the time with 2 stripes and 33% if the model has 3 stripes. The general form is: $\frac{(n-1)^{N-1}}{n^N}$ where n is the number of stripes and where N is the set size.For a quick intuition, we assume that the first item is gated into any one of the stripes. We then multiply two probabilities: 1) the probability that the second item is gated anywhere *except* where the first item was stored - which is $n - 1/n$ for 1 additional item. This probability is multiplied as many times based on the size size minus 1 since the first item is already stored (the power is $N - 1$) 2) The probability that the first item is gated out correctly, which is $1/n$. The probability of this correct guess goes down as the number of stripes increases. The difficulty also increases with set size because the network must learn where to input and output gate for each item, and it is also possible for it to overwrite information by updating a stripe. As such, using a smaller number of stripes but allowing for chunking provides a lossy compression strategy that can mitigate this problem and render credit assignment easier, despite the loss of precision. Rather than overwriting information, the network can learn to use the chunk-linked PFC stripe if it is predictive of task success (minimal cost in the reward function for small errors), and moreover, when chunking is "good enough" the network can leverage repeated reinforcement of the same gating policy to store and read out from the chunked-link PFC stripe, thereby improving credit assignment.

As such, our simulations provide a provocative if somewhat speculative understanding of the nature of WM capacity limitations. It is unlikely that such limitations result from limits in the number of neurons or stripes available in prefrontal cortex, given that discrete estimates on capacity limitations range in the order of 3-4 items whereas the number of stripes (or equivalent clusters of PFC populations) is orders of magnitude larger (Frank et al., 2001). Our simulations show that a limiting step is properly utilizing and managing resources to optimize performance (Figure 6), and that it might actually be more effective to limit the number of representations used. Increasing model capacity to 4 and 8 stripes and the resulting comparisons show that the limitation in the model is not simply about number of slots but the complexity of learning. Using WM requires multiple input and output gating decisions and strategies in tandem with solving and learning a task - this would become trivial with a homunculous dictating what information to store and where to store it. In biology, the PFC has to *learn* these gating strategies: it is not hardwired. This set of experiments helps explain various other WM findings which suggest that effective WM capacity is not just about "capacity" but rather is also about the ability to filter out irrelevant information, the importance of the task (reward), and experience with the task (experts vs. novice) (Astle et al., 2014; Feldmann-Wüstefeld & Vogel, 2019; McNab & Klingberg, 2008; Nakajima et al., 2019; Nassar et al., 2018). It also accords with our findings that when exceeding capacity, networks often "gave up" in the sense that they had more trials in which at least one stripe was empty, due to the influence of negative prediction errors punishing gating policies. As such, we showed that networks require a larger dopamine burst than dip to succeed with increasing task demands. This finding also accords with related data in rodents and our network model in the motor domain, whereby dopamine depletion can cause a progressive 'unlearning' of adaptive strategies (i.e., "giving up") via aberrant NoGo learning (Beeler et al., 2012). This learned Parkinsonism was shown to be related to plasticity in D2 medium spiny neurons (Beeler et al., 2012), and this mechanism was recently confirmed to depend on the indirect pathway (Cheung, Ding, Zhuang, & Kang, 2023).

More generally, our simulations revealed an important role for RL in shaping gating policies as a function of task demands, mimicking normative analysis showing that optimal chunking criterion changes with set size (Nassar et al., 2018). In the network, dopamine is a critical component of RL by adjusting synaptic weights into striatal modules that support input and output gating. The need for a healthy balanced dynamic range of DA signals for adaptive performance provides a potential window into a mechanism that can explain deficits in patient populations with altered striatal DA signaling. Whereas much of the literature in patients with schizophrenia and ADHD focuses on limitations in WM capacity, our simulations suggest an alternative whereby altered DA signaling in these populations (Maia & Frank, 2017) could influence chunking and efficient use of resources. Future work in these patient populations could aim to study these nuances for better understanding of their cognitive deficits.

Limitations and Future Directions

There are several limitations to this work. For simplicity, we restricted our simulations to a chunking network with just one chunk-linked PFC stripe and one or more input stripes. In this case, the determining factor for whether stimuli are merged in the chunking layer depends on how close they are in color, lateral inhibition in the chunking layer, and the relative strength of top-down PFC projections to the chunk layer.

These parameters were fixed in our simulations and were not formally optimized. A more general model could include multiple chunking layers with a reservoir of effective chunking thresholds. Depending on the task, the model could learn to chunk more liberally (larger set size - larger threshold) or more restrictively (smaller set size - smaller threshold), by adapting gating policies to rely on PFC stripes linked to these finer or coarser representations. Alternatively, it is possible that a network could learn to adapt these hyperparameters directly within the chunking layer. Further, through development the brain learns the environmental statistics and could learn those threshold parameters on a developmental time scale and could be fine-tuned on a task by task basis. Our objective was to explore how far one can get by optimizing only the gating policy via biologically plausible RL rules explored widely in basal ganglia.

Because of its wide application in the literature, we considered tasks in which stimuli can be chunked along a single scalar dimension (color or orientation, both of which have shown evidence for chunking Nassar et al. (2018)). Future work should explore to what degree these principle could generalize to more complex stimuli where chunking could occur across other more abstract dimensions, depending on the task demands (Kiyonaga et al., 2017). This model has the potential to be scaled up and here we show the core principles for how the chunking gating strategy can be learned via RL.

One key difference is how the task is presented to the model and to humans. Humans are given clear verbal instructions and are able to perform the color wheel task with little to no practice. However, the model does not receive verbal communication and must learn the task from scratch - random weights. It has no prior experience with how to process the stimuli or how to maintain any stimuli. Humans learn this through development and establish a general gating policy. In a everyday setting, while individuals are not re-learning connections and gating policies to fit individual tasks, they are "fine-tuning" how they manipulate the information in WM and how to apply their learned policies to adapt to the current task. Experimental results show how reward or task relevance are factors that can tweak gating policies ((Nassar et al., 2018; O'Reilly & Frank, 2006)).

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