

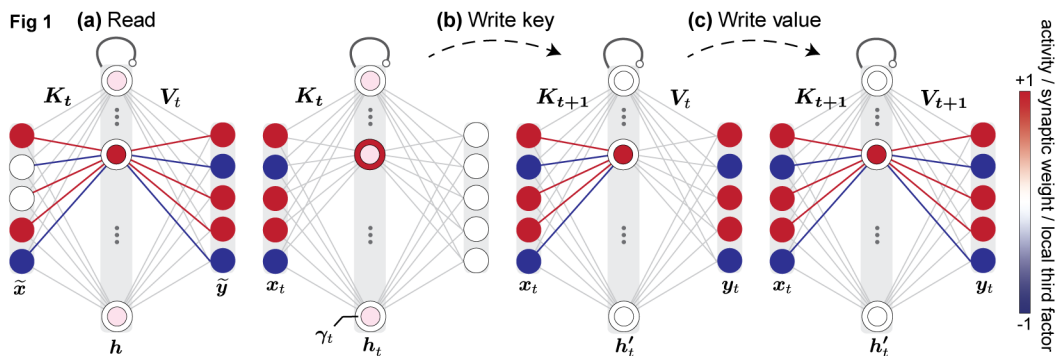
Biological learning in key-value memory networks

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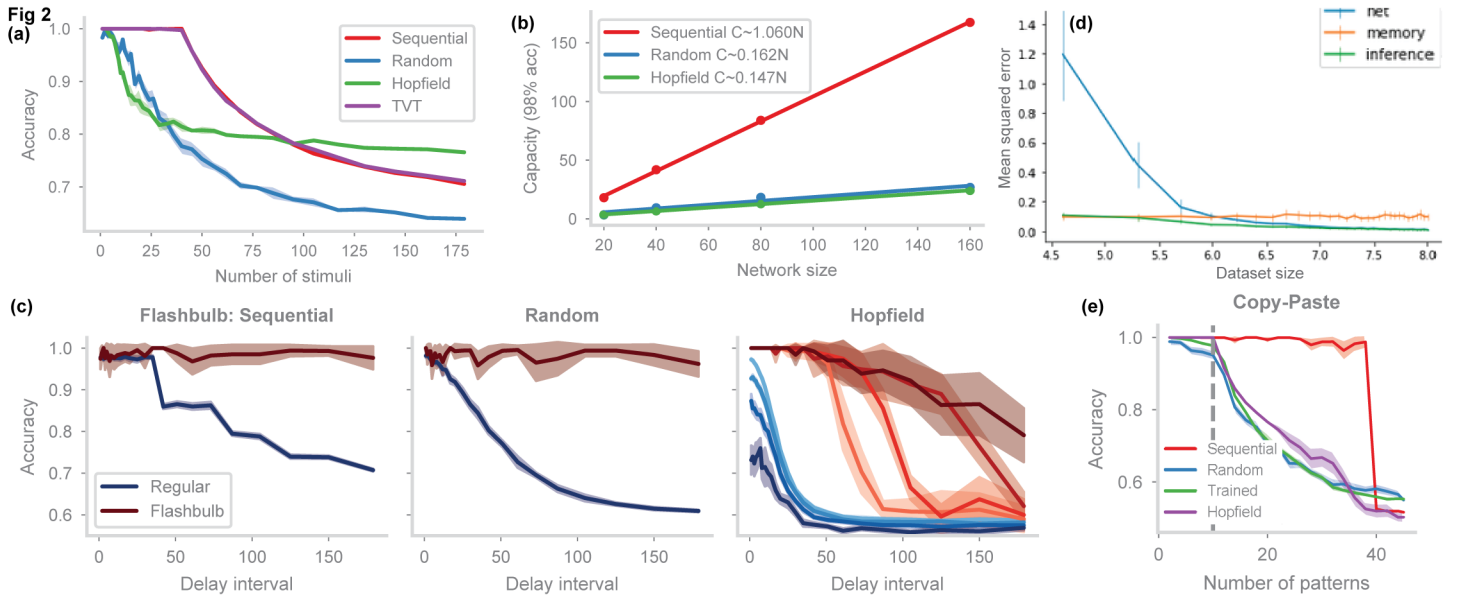
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In neuroscience, classical Hopfield networks are the standard biologically plausible model of long-term memory, relying on Hebbian plasticity for storage and attractor dynamics for recall. In contrast, memory-augmented neural networks in machine learning commonly use a key-value mechanism to store and read out memories in a single step. Such augmented networks achieve impressive feats of memory compared to traditional variants, yet it remains unclear whether they can be implemented by biological systems. In our work, we bridge this gap by proposing a set of biologically plausible three-factor plasticity rules for a basic feedforward key-value memory network. Keys are stored in the input-to-hidden synaptic weights by a "non-Hebbian" rule, controlled only by pre-synaptic activity, and modulated by local third factors which represent dendritic spikes. Values are stored in the hidden-to-output weights by a Hebbian rule, with the pre-synaptic neuron selected through softmax attention which represents recurrent inhibition. The same rules are recovered when network parameters are meta-learned. Our network performs on par with classical Hopfield networks on autoassociative memory tasks and can be naturally extended to correlated inputs, continual recall, heteroassociative memory, and sequence learning. Importantly, since memories are stored in slots indexed by hidden layer neurons, unlike the fully distributed representation in the classical Hopfield network, they can be individually selected for extended storage or rapid decay. Finally, our memory network can easily be incorporated into a larger neural system, either as a memory bank for an external controller, or as a fast learning system used in conjunction with a slow one. Overall, our results suggest a compelling alternative to the classical Hopfield network as a model of biological long-term memory.

Additional Detail. Neural networks capable of long-term memory have been studied in both neuroscience and machine learning, yet a wide gap remains between the mechanisms and interpretations of the two traditions. In neuroscience, long-term associative memory is classically modeled by the Hopfield network [Hopfield, 1982], which stores memories using Hebbian plasticity and retrieves them through recurrent attractor dynamics. In machine learning, memory networks can augment traditional neural networks [Graves et al., 2014, Sukhbaatar et al., 2015, Munkhdalai et al., 2019, Le et al., 2019, Bartunov et al., 2019], providing a stable external memory analogous to computer memory, in contrast to more volatile storage such as recurrent activity. Memory in this tradition can be viewed as consisting of slots, each of which is addressed with a *key* and returns a memory *value*, although this storage scheme commonly lacks a biological interpretation. Prior work on "modern" Hopfield networks [Krotov and Hopfield, 2020, Ramsauer et al., 2020] suggests a neural architecture for readout, but lacks a biological writing mechanism. We introduce a biologically plausible learning rule that uses local three-factor synaptic plasticity [Gerstner et al., 2018] and respects the topological constraints of biological neurons with spatially separated dendrites and axons.



A basic key-value memory (KVM) contains a key and a value matrix $\mathbf{K}_t, \mathbf{V}_t$, corresponding to input-to-hidden and hidden-to-output synaptic weights. Given a query \tilde{x} it retrieves output $\mathbf{y} = \mathbf{V}_t \mathbf{h}$, where $\mathbf{h} = f(\mathbf{K}_t \tilde{x})$ is the hidden response and f is an activation function over the dot-product similarities between



$\tilde{\mathbf{x}}$ and the rows of \mathbf{K}_t . We use $f(\cdot) = \text{softmax}(\cdot)$, which sparsifies the hidden layer and can be approximated biologically by recurrent inhibition (Fig 1a). A new input \mathbf{x}_t is written into slot i of the key matrix (presynaptic weights of hidden neuron i) using a non-Hebbian plasticity rule dependent on presynaptic activity, $\mathbf{K}_{t+1} = (1 - \eta_t^K) \odot \mathbf{K}_t + \eta_t^K \odot (\mathbf{1}\mathbf{x}_t^T)$, where $\mathbf{1} \equiv (1, 1, \dots, 1)$, with learning rate $[\eta_t^K]_{ij} = q_t[\gamma_t]_i$. A local third factor (LTF) $[\gamma_t]_i \in \{0, 1\}$ gates the plasticity of all input connections to hidden unit i , enabling selection of a single neuron for writing (e.g. a dendritic spike, as in hippocampal behavioral time scale plasticity [Bittner et al., 2017]). A scalar global third factor (GTF) $q_t \in \{0, 1\}$ (e.g. global neuromodulator) gates whether a stimulus is stored at all (Fig 1b). Having stored \mathbf{x}_t in slot i of \mathbf{K}_{t+1} , the hidden layer activity is now $\mathbf{h}'_t = \text{softmax}(\mathbf{K}_{t+1}\mathbf{x}_t)$. If \mathbf{x}_t is uncorrelated with previously stored keys, \mathbf{h}'_t is approximately one-hot, with $[\mathbf{h}'_t]_i \approx 1$. The output layer activity is then clamped to the target \mathbf{y}_t (e.g. by residual input-to-output connections) and which is stored in slot i (postsynaptic weights of hidden unit i) of the value matrix by a Hebbian rule $\mathbf{V}_{t+1} = (1 - \eta_t^V) \odot \mathbf{V}_t + \eta_t^V \odot \mathbf{y}_t(\mathbf{h}'_t)^T$ with $[\eta_t^V]_{ki} = q_t$ (Fig 1c). Importantly, if the update rules are *meta-learned* by gradient descent, similar non-Hebbian and Hebbian rules emerge.

To evaluate performance, we consider the classical autoassociative recall task where the network stores a set of stimuli and the query is a corrupted version of a stored key. Our network with sequentially or randomly chosen LTFs shows similar performance to the classical Hopfield network when measuring accuracy as a function of the number of stimuli (Fig 2a). By design, "sequential" performs identically to a simple non-biological KVM (TVT, [Hung et al., 2019]). We further demonstrate similar results for temporally correlated stimuli, for *heteroassociative* recall, and for a continual analogue of this task. The capacity (maximum number of stimuli stored with 95% accuracy) of both versions of our model scales linearly with the number of hidden neurons, like Hopfield (Fig 2b), but has the advantage of decoupling the size of the input from the storage dimension (hidden layer). Additionally, to demonstrate utility of the factorized structure of KVM, we consider "flashbulb" memories, a phenomenon where highly salient experiences are remembered with extreme efficacy, often for life. In a continual recall task, a subset of the inputs are selected as flashbulb memories and maintained in memory by a simple meta-plasticity mechanism, resulting in longer memory lifetimes while maintaining performance on regular ones (Fig 2c). Next, we consider KVM in conjunction with a gradient-based network to learn smooth functions (Fig 2d). With few samples, the fast-learning memory outperforms the slower gradient network, but with more samples the slower network generalizes. Linearly weighting the outputs based on their confidence (entropy of hidden layer in KVM, and dropout variance in the gradient net) allows inference of the output better than either one alone. Finally, we consider using KVM as a memory bank for an external controller (Fig 2e). In the "copy-paste" task, the system's goal is to autonomously reproduce a sequence of stimuli. A feedforward network generates keys/values to be stored in the memory bank, as well as the GTF for controlling writing. The "sequential"

memory has near-perfect performance until it reaches storage capacity, and the hand-tuned or meta-learned "random" ones perform on-par with Hopfield. Overall, our learning rules suggest a biologically plausible alternative for the classical Hopfield network as a model of long-term memory, with the high performance and flexibility of key-value memory used in machine learning.

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