

1 **Sleep prevents catastrophic forgetting in spiking neural networks by**  
2 **forming joint synaptic weight representations**

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21

## 22 **Abstract (150 max)**

23 Artificial neural networks overwrite previously learned tasks when trained sequentially, a  
24 phenomenon known as catastrophic forgetting. In contrast, the brain learns continuously, and  
25 typically learns best when new learning is interleaved with periods of sleep for memory  
26 consolidation. In this study, we used spiking network to study mechanisms behind catastrophic  
27 forgetting and the role of sleep in preventing it. The network could be trained to learn a complex  
28 foraging task but exhibited catastrophic forgetting when trained sequentially on multiple tasks.  
29 New task training moved the synaptic weight configuration away from the manifold representing  
30 old tasks leading to forgetting. Interleaving new task training with periods of off-line  
31 reactivation, mimicking biological sleep, mitigated catastrophic forgetting by pushing the  
32 synaptic weight configuration towards the intersection of the solution manifolds representing  
33 multiple tasks. The study reveals a possible strategy of synaptic weights dynamics the brain  
34 applies during sleep to prevent forgetting and optimize learning.

35

## 36 **Introduction**

37 Humans are capable of continuously learning to perform novel tasks throughout life without  
38 interfering with their ability to perform previous tasks. Conversely, while modern artificial  
39 neural networks (ANNs) are capable of learning to perform complicated tasks, ANNs have  
40 difficulty learning multiple tasks sequentially<sup>1-3</sup>. Sequential training commonly results in  
41 catastrophic forgetting, a phenomenon which occurs when training on the new task completely  
42 overwrites the synaptic weights learned during the previous task, leaving the ANN incapable of  
43 performing a previous task<sup>1-4</sup>. Attempts to solve catastrophic forgetting have drawn on insights

44 from the study of neurobiological learning, leading to the growth of neuroscience-inspired  
45 artificial intelligence (AI)<sup>5-7</sup>. While these approaches are capable of mitigating catastrophic  
46 forgetting in certain circumstances<sup>6</sup>, a general solution which can achieve human level  
47 performance for continual learning is still an open question.

48 Historically, an interleaved training paradigm, where multiple tasks are presented within  
49 a common training dataset, has been employed to circumvent the issue of catastrophic  
50 forgetting<sup>4,8,9</sup>. In fact, interleaved training was originally construed to be an approximation to  
51 what the brain may be doing during sleep to consolidate memories; spontaneously reactivating  
52 memories from multiple interfering tasks in an interleaved manner<sup>9</sup>. Unfortunately, explicit use  
53 of interleaved training, in contrast to memory consolidation during biological sleep, imposes the  
54 stringent constraint that the original training data be perpetually stored for later use and  
55 combined with new data to retrain the network<sup>1,2,4,9</sup>. Thus, the challenge is to understand how the  
56 biological brain enables memory reactivation during sleep without access to past training data.

57 Parallel to the growth of neuroscience-inspired ANNs, there has been increasing  
58 investigation of spiking neural networks (SNNs) which attempt to provide a more realistic model  
59 of brain functioning by taking into account the underlying neural dynamics and by using  
60 biologically plausible local learning rules<sup>10-13</sup>. A potential advantage of the SNNs, that was  
61 explored in our new study, is that local learning rules combined with spike-based communication  
62 allow previously learned memory traces to reactivate spontaneously and without interference  
63 during off-line processing – sleep. A common hypothesis, supported by a vast range of  
64 neuroscience data, is that the consolidation of memories during sleep occurs through local  
65 unsupervised synaptic changes enabled by reactivation of the neuron ensembles engaged during

66 learning<sup>14</sup>. Indeed, spike sequence replay was observed in the neocortex<sup>15-17</sup> following both  
67 hippocampal-dependent tasks<sup>15</sup> and hippocampal-independent tasks<sup>18</sup>.

68 Here we used a multi-layer SNN with reinforcement learning to investigate whether  
69 interleaving periods of new task training with periods of noise-induced spontaneous reactivation,  
70 resembling sleep in the brain<sup>19-21</sup>, can circumvent catastrophic forgetting. The network could be  
71 trained to learn one of two complementary complex foraging tasks involving pattern  
72 discrimination but exhibits catastrophic forgetting when trained on the tasks sequentially.  
73 Significantly, we show that catastrophic forgetting can be prevented by periodically interrupting  
74 reinforcement learning on a new task with unsupervised sleep phases. While new task training  
75 alone moved synaptic weight configuration away from the solution manifold representing old  
76 tasks and towards the manifold specific for new task, interleaving new task training with  
77 unsupervised sleep replay allowed the synaptic weights to stay near the manifold specific for the  
78 old task and still to move towards its intersection with the manifold representing the new task.  
79 Our study predicts that sleep prevents catastrophic forgetting in the brain by forming joint  
80 synaptic weight representations suitable for storing multiple memories.

81

## 82 **Results**

### 83 **Complementary complex foraging tasks can be robustly learned**

84 We modeled a simple 3-layer feedforward spiking neural network (see Figure 1A and *Methods:*  
85 *Network Structure* for details) simulating basic steps from sensory input to motor output in the  
86 brain. Excitatory synapses between the input (I) and hidden (H) layers were subjected to  
87 unsupervised learning (implemented as non-rewarded STDP)<sup>22,23</sup> while those between the H and

88 output (O) layers were subjected to reinforcement learning (implemented using rewarded  
89 STDP)<sup>24-27</sup> (see *Methods: Synaptic plasticity* for details). Unsupervised plasticity allowed  
90 neurons in layer H to learn different particle patterns at various spatial locations of the input  
91 layer I, while rewarded STDP allowed the neurons in layer O to learn motor decisions based on  
92 the type of the particle patterns detected in the visual field<sup>12</sup>. We trained the network on one of  
93 two complementary complex foraging tasks. In either task, the network learned to discriminate  
94 between a rewarded and a punished particle pattern in order to acquire as much of the rewarded  
95 patterns as possible. In the following we consider pattern discriminability (rewarded vs  
96 punished) as a measure of performance, with chance performance being 0.5.

97         The paradigm for Task 1 is shown in Figure 1B. First, during an unsupervised learning  
98 period, all 4 types of 2-particle patterns (horizontal, vertical, positive diagonal, and negative  
99 diagonal) were present in the environment with equal densities. This was a period, equivalent to  
100 a developmental critical period in the brain, when the network learned the environmental  
101 statistics and formed, in layer H, high level representation of all possible patterns found at the  
102 different visual field locations (see Figure 2 for details). Unsupervised training was followed by  
103 a reinforcement learning period, equivalent to task specific training in the brain, during which the  
104 synapses between layers I and H were frozen but synapses from H to O were updated using a  
105 rewarded STDP rule. The reinforcement learning period was when the network learned to make  
106 decisions about which direction to move based on the visual input. Whether patterns were  
107 rewarded during reinforcement learning depended on the task – for Task 1 horizontal patterns  
108 were rewarded and negative diagonal patterns were punished (Figure 1D). During both the  
109 rewarded training and the testing periods only 2 types of patterns were present in the  
110 environment (e.g. horizontal and negative diagonal for Task 1).

111           After training Task 1, mean performance on Task 1 was  $0.70 \pm 0.2$  while on Task 2  
112 (which has not been trained yet) was  $0.53 \pm 0.2$  (chance level). Figure 1D shows examples of  
113 trajectories of the simulated agent at the beginning of (left) and after (right) reinforcement  
114 learning period. The naive agent moved randomly through the environment, but after training it  
115 moved to seek out horizontal patterns and largely avoid negative diagonal ones. The  
116 complementary paradigm for Task 2 (vertical patterns are rewarded and positive diagonal are  
117 punished) is shown in Figure 1C,E. These results demonstrate that the network is capable of  
118 learning and performing either one of the two complementary complex foraging tasks.

119           To get an understanding of the policy developed by the network for each task, we  
120 computed the receptive field of each neuron in layer O with respect to the input from layer I (see  
121 schematic in Figures 2A/C) . This was done by first computing the receptive fields of all of the  
122 neurons in layer H with respect to I, then performing a weighted average where the weights were  
123 given by the synaptic strength from each neuron in layer H to the particular neuron in layer O.  
124 Figure 2A shows a representative example of the receptive field which developed after training  
125 on Task 1 for one specific neuron in layer O which controls movements to the upper-left  
126 direction. This neuron responded most robustly to bars of horizontal orientation (rewarded) in the  
127 upper-left quadrant of the visual field and, importantly, did not respond to bars of negative  
128 diagonal orientation (punished).

129           Figure 2B shows examples of receptive fields of six neurons in layer H which synapse  
130 strongly onto the upper-left neuron in layer O (the neuron shown in Figure 2A). These neurons  
131 form high level representations of the input patterns, similar to the neurons in the higher levels of  
132 the visual system or later layers of a convolutional neural network<sup>28-30</sup>. The majority of these  
133 receptive fields revealed strong selection for the horizontal (i.e. rewarded) food particles in the

134 upper-left quadrant of the visual field. As a particularly notable example, one of these layer H  
135 neurons (Figure 2B; middle-right) preferentially responded to negative diagonal (i.e. punished)  
136 food particles in the bottom-right quadrant of the visual field. Thus, spiking in this neuron caused  
137 the agent to move away from these punished food particles. Similar findings after training on  
138 Task 2 are shown in Figures 2C and 2D.

139

### 140 **Catastrophic forgetting occurs following sequential but not interleaved training**

141 We next tested whether the network model could exhibit catastrophic forgetting by training  
142 sequentially on Task 1 (old task here) followed by Task 2 (new task) (Figure 3A). Following  
143 Task 2 training, performance on Task 1 was down to no better than chance ( $0.52 \pm 0.02$ ), while  
144 performance on Task 2 improved to  $0.69 \pm 0.03$  (Figure 3 A,B). Thus, sequential training on a  
145 complementary task caused the network to undergo catastrophic forgetting of the task trained  
146 earlier, remembering only the most recent task.

147 Interleaved training was proposed as a solution for catastrophic forgetting<sup>4,8,9</sup>, so we  
148 added an Interleaved Task 1 and Task 2 (Interleaved<sub>T1,T2</sub>) training phase to our simulation  
149 (Figure 3A) to test whether it was capable of learning Task 1 (now new task) without  
150 overwriting Task 2 (old task). For interleaved training we alternated short presentations of Task  
151 1 and Task 2 every 100 movement cycles. Figure 3B shows that, following Interleaved<sub>T1,T2</sub>  
152 training, the network achieved a performance of  $0.65 \pm 0.03$  on Task 1 and a performance of  
153  $0.67 \pm 0.04$  on Task 2. Therefore, Interleaved<sub>T1,T2</sub> training allowed the network to relearn Task 1  
154 without forgetting what the network had just learned during training on Task 2. Note, we also  
155 tested Interleaved<sub>T1,T2</sub> training right after the unsupervised phase and found the same high  
156 performance for both Task 1 and Task 2 (not shown).

157 We identified task-relevant synapses after training on a given task (top 10% of synapses),  
158 and we traced the same set of synapses after training on the opposing task or after  
159 Interleaved<sub>T1,T2</sub> training. The structure in the distribution of Task 1-relevant synapses following  
160 Task 1 training (Figure 3C, top-left) was destroyed following Task 2 training (top-middle; i.e.,  
161 majority of Task 1-relevant synapses were reduced to zero after Task 2 training) but partially  
162 recovered following Interleaved<sub>T1,T2</sub> training (top-right). Similarly, the structure in the  
163 distribution of Task 2-relevant synapses following Task 2 training (bottom-middle) was not  
164 present following Task 1 training (bottom-left) and was partially retained following  
165 Interleaved<sub>T1,T2</sub> training (bottom-right).

166 To better understand the effect of Interleaved<sub>T1,T2</sub> training on the synaptic weights, we  
167 trained a support vector machine (SVM; see *Method: Support Vector Machine Training* for  
168 details) with a radial basis function kernel to classify the synaptic weight configurations between  
169 layers H and O (i.e. those responsible for decision making) according to whether they serve to  
170 perform Task 1 or Task 2. Figure 3D shows the average distance from the decision boundary  
171 across trials for synaptic weights associated with Task 1, Task 2, and Interleaved<sub>T1,T2</sub> training.  
172 While the SVM robustly classified the synaptic weight matrices from Task 1 and Task 2, the  
173 weight states after Interleaved<sub>T1,T2</sub> training were significantly closer to the decision boundary  
174 (typically on the task 2 side). This indicates that the synaptic weight matrices from  
175 Interleaved<sub>T1,T2</sub> training are a mixture of Task 1 and Task 2 states.

176 Figure 3E shows the trajectory of the synaptic weight distribution for the experiment in  
177 Figure 3A projected to 3-dimensions using principal components analysis (PCA). It can be seen  
178 that while synaptic weight matrices associated with Task 1 and Task 2 training cluster in distinct



179 regions of PC space, Interleaved<sub>T1,T2</sub> training pushes the synaptic weights to an intermediate  
180 location between Task 1 and Task 2.

181

## 182 **Periods of sleep allow for sequential training without catastrophic forgetting**

183 Sleep is believed to be an off-line processing period when recent memories are replayed to avoid  
184 damage by new learning. Particularly for procedural (hippocampal-independent) memories,  
185 rapid-eye-movement (REM) sleep may organize neuronal activity to replay memory traces<sup>31</sup>.

186 Can we implement a sleep like phase to our model to protect an old task and still accomplish new  
187 task learning without explicit re-training of the old task (e.g., without doing explicit interleaved  
188 training of Task 1 and Task 2)?

189         Again, we first trained the network on Task 1 and Task 2 sequentially to illustrate  
190 occurrence of catastrophic forgetting (Figure 4A). At this point the network remembered the  
191 most recent task (i.e. Task 2) but Task 1 was forgotten. Next, we implemented a training phase  
192 consisted of alternating periods of training on Task 1 (considered to be a new task here) lasting  
193 100 movement cycles and periods of “sleep” of the same duration (we will refer to this training  
194 phase as Interleaved<sub>S,T1</sub>). To simulate sleep, the rewarded STDP rule was replaced by  
195 unsupervised STDP, ensuring a truly offline learning period, and hidden layer neurons were  
196 artificially stimulated by Poisson distributed spike trains in order to maintain spiking rates  
197 similar to that during task training (indeed, in vivo, activity of the neocortical neurons during  
198 REM sleep is similar to awake<sup>32</sup>; see *Methods: Simulated Sleep* for details). Importantly, no  
199 training on Task 2 (old task here) was performed at any time during Interleaved<sub>S,T1</sub>. Figure 4B  
200 shows that following Interleaved<sub>S,T1</sub> the network achieved a performance of  $0.69 \pm 0.02$  on Task  
201 1 and a performance of  $0.67 \pm 0.03$  on Task 2, comparable to both single task performances

202 following sequential training on Task 1 ( $0.70 \pm 0.02$ ) and Task 2 ( $0.69 \pm 0.03$ ) (Figure 1B/C) and  
203 exceeding those achieved through Interleaved<sub>T1,T2</sub> training (Figure 3B). When durations of Task  
204 1 individual training episodes was increased significantly beyond 100 cycles during  
205 Interleaved<sub>S,T1</sub>, the network was only able to perform well on the new Task 1 while performance  
206 on the old Task 2 dropped to the chance level (not shown).

207 We interpret these results as follows (see sections below for detailed synaptic  
208 connectivity analysis). Each episode of new Task 1 training improves Task 1 performance but  
209 damages synaptic connectivity responsible for old Task 2. If continuous Task 1 training is long  
210 enough, the damage to Task 2 becomes irreversible. Having a sleep phase after a short period of  
211 Task 1 training enables spontaneous forward (H->O) replay that preferentially benefits the  
212 strongest synapses. Thus, if Task 2 synapses are still strong enough, they are replayed and  
213 increase. To keep the protocol consistent with our previous experiments on Interleaved<sub>T1,T2</sub>  
214 training, we used a combination of sleep and Task 1 training – the same task that was initially  
215 trained to naïve network but overwritten during Task 2 training (i.e., entire sequence of events  
216 was T1 -> T2 -> Interleaved<sub>S,T1</sub>). However, we obtained the same results in an experiment when,  
217 after initial Task 1 training, Task 2 training was interleaved with sleep (i.e., T1 ->  
218 Interleaved<sub>S,T2</sub>), which prevented forgetting Task 1 while Task 2 was learned (see Extended Data  
219 Figure 1).

220 We next traced “task-relevant” synapses, i.e. synapses identified in the top 10%  
221 distribution following training on that specific task (Figure 4C; compare to Figure 3C for  
222 Interleaved<sub>T1,T2</sub> training). The structure in the distribution of Task 1-relevant synapses following  
223 Task 1 training (Figure 4C; top-left) was destroyed following Task 2 training (top-middle) but  
224 partially recovered following Interleaved<sub>S,T1</sub> training (top-right). The structure in the distribution

225 of Task 2-relevant synapses following Task 2 training (bottom-middle) was not present  
226 following Task 1 training (bottom-left) and was partially retained following Interleaved<sub>S,T1</sub>  
227 training (bottom-right). Thus, sleep can preserve important synapses while incorporating new  
228 ones.

229 Figure 4D shows that the SVM robustly classified the synaptic weight states from Task 1  
230 and Task 2 while those from Interleaved<sub>S,T1</sub> weight states fell significantly closer to the decision  
231 boundary. This indicates that, similar to Interleaved<sub>T1,T2</sub>, the synaptic weight matrices which  
232 result from Interleaved<sub>S,T1</sub> training are a mixture of Task 1 and Task 2 states. The trajectory of  
233 the synaptic weights in PC space shown in Figure 4E provides a visualization of these dynamics.  
234 Importantly, the smoothness of this trajectory to its steady state suggests that Task 2 information  
235 is never completely erased during this evolution. We take this as evidence that Interleaved<sub>S,T1</sub>  
236 training is capable of integrating synaptic information relevant to Task 1 while preserving Task 2  
237 information.

238

### 239 **Receptive fields of decision-making neurons after sleep represent multiple tasks**

240 To observe that the network has learned both tasks after Interleaved<sub>S,T1</sub> training, we mapped the  
241 receptive fields of decision-making neurons in layer O (Figure 5; see Figure 2 for comparison).  
242 Figure 5A shows the receptive field for the neuron in layer O which controls movement in the  
243 upper-left direction. This neuron responds to both horizontal (rewarded for Task 1) and vertical  
244 (rewarded for Task 2) orientations in the upper-left quadrant of the visual field. Although it  
245 initially appears that this layer O neuron may also be responsive to diagonal patterns in this  
246 region, analysis of the receptive fields of neurons in layer H (Figure 5B) revealed that these  
247 receptive fields are selective to either horizontal food particles (left; rewarded for Task 1) or

248 vertical food particles (right; rewarded for Task 2) in the upper-left quadrant of the visual field.  
249 Other receptive fields were responsible for avoidance of punished particles for both tasks (see  
250 examples in Figure 5B, bottom-middle-right and bottom-middle-left). Thus, the network will  
251 utilize one of two distinct sets of layer H neurons, selective for either Task 1 or Task 2,  
252 depending on which food particles are present in the environment.

253

### 254 **Periods of sleep allow reintegration of new task without interference through** 255 **renormalization of task-relevant synapses**

256 To visualize synaptic weight dynamics during Interleaved<sub>S,T1</sub> training, traces of all synapses  
257 projecting to a single representative output layer neuron were plotted (figure 6A). At the onset of  
258 Interleaved<sub>S,T1</sub> training (i.e. 240,000 aeons), the network was only able to perform on Task 2,  
259 meaning the strong synapses in the network were specific to this task. These synapses were  
260 represented by a cluster ranging from ~0.08 to ~0.4; the rest of synapses grouped near 0. As  
261 Interleaved<sub>S,T1</sub> training progressed, Task 1 specific synapses moved to the strong cluster and  
262 some, presumably less important, Task 2 synapses moved to the weak cluster. After a period of  
263 time the rate of transfer decreased and the total number of synapses in each group stabilized,  
264 showing that the network is approaching equilibrium (Figure 6B).

265 To visualize how sleep renormalizes task relevant synapses, we plotted two-dimensional  
266 weight distributions for Task 1->Task2 (Figure 6C) and Task 2 -> Interleaved<sub>S,T1</sub> (Figure 6D)  
267 experiments (see *Methods: 2-D Synaptic Weight Distributions* for details). To establish a  
268 baseline, in Figure 6C (left) the weight state at the end of Task 1 training (X-axis) (see overall  
269 timeline of this experiment in Figure 4A) was compared to itself (Y-axis). This formed a  
270 perfectly diagonal plot. Most synapses were weak (red dots) with stronger synapses forming a

271 tail in the distribution. The next comparison (Figure 6C, middle) was between the weight state  
272 after Task 1 training (X-axis) and a time early on Task 2 training (Y-axis). At that time, synapses  
273 were only able to modify their strength slightly, causing most points to lie close to the diagonal.  
274 As training on Task 2 continued until maximum performance was reached, synapses moved far  
275 away from the diagonal (Figure 6C, right). Two trends were observed. A set of synapses that had  
276 a strength near zero following Task 1 training increased strength following Task 2 training  
277 (Figure 6D, right, red dots along Y-axis). At the same time, many strongly trained by Task 1  
278 synapses were depressed down to zero (Figure 6C, right, red dots along X-axis). The latter  
279 illustrates the effect of catastrophic forgetting - complete overwriting of the synaptic weight  
280 matrix caused performance of Task 1 to return to baseline after training on Task 2.

281 Does sleep prevent overwriting of the synaptic weight matrix? The Figure 6D plots use  
282 the weight state at the end of training Task 2 as a reference that is compared to different times  
283 during Interleaved<sub>S,T1</sub> training. The first two plots (Figure 6D, left/middle) are similar to those in  
284 Figure 6C. However, after Interleaved<sub>S,T1</sub> training (Figure 6D, right) many synapses that were  
285 strong following Task 2 training were not depressed to zero but rather were pushed to an  
286 intermediate strength where they are still functional (note cluster of points parallel to X-axis; see  
287 also projection to 1D on the right side of the graph). Thus, Interleaved<sub>S,T1</sub> training, combining  
288 new training on Task 1 with periods of unsupervised sleep, moved synapses in a way that  
289 preserved strong synapses from a previously learned task while also introducing new strong  
290 synapses to perform a new task. Since a significant fraction of the strong synapses from training  
291 on Task 2 were preserved (due to the sleep periods), performance on Task 2 remained high  
292 following Interleaved<sub>S,T1</sub> training despite the fact that the networks received no new training  
293 examples of Task 2.

294

295 **Periods of sleep push the network towards the intersection of the solution manifolds**  
296 **representing Task 1 and Task 2 specific weight configurations**

297 To visualize the approximate task-specific solution manifolds ( $M_{T1}$  and  $M_{T2}$ ) and their  
298 intersection ( $M_{T1 \cap T2}$ ) in synaptic weight space, we used multiple trials (with different  
299 initialization) of Task 1 and Task 2 training to sample the manifolds. Figure 7A shows (in kPCA  
300 space) that multiple different configurations of synaptic weights can provide high performance  
301 for a given task. For example, all red dots in Figure 7A represent the states with the same high  
302 level of performance for Task 1 (but not Task 2). In addition, cyan and green dots represent  
303 states with high level of performance for both Task 1 and Task 2. We interpret these results as  
304 evidence that synaptic weight space includes a manifold,  $M_{T1}$ , where different configurations of  
305 weights (red, green, cyan dots) all allow for Task 1 to perform well. This manifold intersects  
306 with another one,  $M_{T2}$ , where different weights configurations (blue, green, cyan dots) are all  
307 suitable for Task 2. Figures 7B and 7C show 2D projections of this space onto PCs 1 and 2 and  
308 PCs 1 and 3, respectively. From these projections, we can see that PC 1 seems to capture the  
309 extent to which a synaptic weight configuration is associated with Task 1 (positive values) or  
310 Task 2 (negative values), while PC 2 and PC 3 capture the variance in synaptic weight  
311 configurations associated with Task 1 and Task 2, respectively. Note, the trajectories through this  
312 space (red/blue lines) during Interleaved<sub>T1,T2</sub> and Interleaved<sub>S,T1/T2</sub> training would also belong to  
313 the respective task manifolds as performance on the old tasks was never lost in these training  
314 scenarios.

315 We calculated the distance from the current synaptic weight configurations to  $M_{T1}$   
316 (Figure 7D),  $M_{T2}$  (Figure 7E), and  $M_{T1 \cap T2}$  (Figure 7F; see *Methods: Distance from Solution*

317 *Manifolds* for details). Figures 7D and 7E show that while Sequential (T1->T2 or T2->T1)  
318 training causes synaptic weight configurations to diverge quickly from its initial solution  
319 manifold (i.e.  $M_{T1}$  or  $M_{T2}$ ), both Interleaved<sub>T1,T2</sub> and Interleaved<sub>S,T1/T2</sub> training cause synaptic  
320 weight configurations to stay close to the initial solution manifold as the new task was learned.  
321 (Note, that we under sampled  $M_{T1}$  and  $M_{T2}$ , which explains initial distance increase.)  
322 Importantly, Figure 7F shows that while both Interleaved<sub>T1,T2</sub> and Interleaved<sub>S,T1/T2</sub> training cause  
323 synaptic weight configurations to smoothly converge towards  $M_{T1 \cap T2}$ , Sequential training avoids  
324 this intersection entirely.

325 In Figure 7G we show a schematic depiction of these results. The task-specific manifolds,  
326  $M_{T1}$  and  $M_{T2}$ , are roughly defined in 3D projection by two orthogonal elliptic paraboloids with  
327 opposite orientation, with an approximately ellipsoidal intersection,  $M_{T1 \cap T2}$ . Figures 7H and 7I  
328 depict the trajectories the network takes in this space following Task 2 and Task 1 training,  
329 respectively. Sequential training causes the network to jump directly from one task-specific  
330 solution manifold to the other, resulting in catastrophic forgetting. In contrast, interleaving new  
331 task training with sleep (Interleaved<sub>S,T1/T2</sub>) prevents catastrophic forgetting by keeping the  
332 network close to the old task solution manifold as it converges towards  $M_{T1 \cap T2}$  – a region capable  
333 a supporting both tasks simultaneously.

334

## 335 **Discussion**

336 In this study we report that a multi-layer SNN utilizing reinforcement learning may exhibit  
337 catastrophic forgetting upon sequential training of two complementary complex foraging tasks,  
338 but the problem is mitigated if the network is allowed, during new task training, to undergo

339 intervening periods of spontaneous reactivation which we consider to be equivalent to the replay  
340 observed during periods of sleep in biological systems. This scenario was effectively equivalent  
341 to explicit interleaved training of both tasks, however, no training data for the old task were  
342 required during “sleep”. At the synaptic level, training a new task alone led to complete  
343 overwriting of synaptic weights responsible for the previous task. In contrast, interleaving  
344 periods of reinforcement learning on a new task with periods of unsupervised learning during  
345 sleep preserved old task synapses damaged by new task training to avoid forgetting and  
346 enhanced new task synapses to allow new task learning. Thus, the network was pushed towards  
347 the intersection of the solution manifolds representing synaptic weight configurations associated  
348 with each task - an optimal compromise for performing both tasks.

349         The critical role that sleep plays in learning and memory is supported by a vast,  
350 interdisciplinary literature spanning both psychology and neuroscience<sup>21,33-36</sup>. Specifically, it has  
351 been suggested that REM sleep supports the consolidation of non-declarative or procedural  
352 memories while non-REM sleep supports the consolidation of declarative memories<sup>21,35,37</sup>. In  
353 particular, REM sleep has been shown to be important for the consolidation of memories of tasks  
354 involving perceptual pattern separation, such as the texture discrimination task<sup>21,38</sup>. Despite the  
355 difference in the cellular and network dynamics during these two stages of sleep<sup>21,35</sup>, both are  
356 thought to contribute to memory consolidation through repeated reactivation, or replay, of  
357 specific memory traces acquired during learning<sup>19-21,33,34,37,39</sup>. These studies suggest that through  
358 replay, sleep can support the process of off-line memory consolidation to circumvent the  
359 problem of catastrophic forgetting.

360         From mechanistic perspective, the sleep phase in our model protects old memories by  
361 enabling unsupervised learning - spontaneous replay of synapses responsible for previously



362 learned tasks. We previously reported that in the thalamocortical models, a sleep phase may  
363 enable replay of spike sequences learned in awake to improve post-sleep performance<sup>39,40</sup> and to  
364 protect old memories from catastrophic forgetting<sup>41</sup>. Although in this work we model sleep and  
365 noise with spiking statistics similar to awake training, theoretical work from another group has  
366 also shown that noise causes implicit rehearsal of older memories which protects against  
367 interference<sup>42</sup>. Here we found, however, that a single episode of new task training using  
368 reinforcement learning could quickly erase an old memory to the point that it cannot be  
369 recovered by subsequent sleep. The solution was similar to how brain slowly learns procedural  
370 (hippocampal-independent) memories<sup>21,35,37,38,43</sup>. Each episode of new task training improves this  
371 task performance only slightly but also damages slightly synaptic connectivity responsible for  
372 the older task. Subsequent sleep phases enable replay that preferentially benefits the strongest  
373 synapses, such as those from old memory traces, to allow them to recover.

374         We found that multiple distinct configurations of synaptic weights can support each task  
375 in our model, suggesting the existence of task specific solution manifolds in synaptic weight  
376 space. Sequential training of new tasks makes the network to jump from one solution manifold to  
377 another, enabling memory for the most recent task but erasing memories of the previous tasks.  
378 Interleaving new task training with sleep phases enables the system to evolve towards  
379 intersection of these manifolds where synaptic weight configurations can support multiple tasks  
380 (a similar idea was recently proposed in the machine learning literature to minimize catastrophic  
381 interference by learning representations that accelerate future learning<sup>44</sup>). From this point of view  
382 having multiple episodes of new task training interleaved with multiple sleep episodes allows  
383 gradual convergence to the intersection of the manifolds representing old and new tasks, while a

384 single long episode of new task learning would push the network far away from the old task  
385 manifold making it impossible to recover by subsequent sleep.

386         Although classical interleaved training showed similar performance results in our model  
387 as interleaving training with sleep, we believe the latter to be superior on the following  
388 theoretical grounds. Classical interleaved training will necessarily cause the system to oscillate  
389 about the optimal location in synaptic weight space which can support both tasks because each  
390 training cycle uses a cost function specific to only a single task. While this can be ameliorated  
391 with a learning rate decay schedule, the system is never actually optimizing for the desired dual-  
392 task state. Sleep, on the other hand, can support not only replays of the old task, but also support  
393 replays which are a mixture of both tasks<sup>42,45,46</sup>. Thus, through unsupervised learning during  
394 sleep replay, the system is able to perform approximate optimization for the desired dual-task  
395 state.

396         While our model represents a dramatic simplification of any biological system, we  
397 believe that it captures some important processing steps of how animal and human brains interact  
398 with the external world. The primary visual system is believed to employ a sequence of  
399 processing steps when visual information is increasingly represented by neurons encoding higher  
400 level features<sup>28-30</sup>. This processing step was reduced to very simple convolution from input to  
401 hidden layer in our model. Subsequently, in the brain, associative areas and motor cortex are  
402 trained to make decisions based on reward signals released by neuromodulatory centers<sup>8,47-49</sup>.  
403 This was reduced in our model to synaptic projections from the hidden to output (decision  
404 making) layer implementing rewarded STDP to learn a task<sup>24-26</sup>.

405         Our results are in line with a large body of literature suggesting that interleaved training  
406 is capable of mitigating catastrophic forgetting in ANNs<sup>4,8,9</sup> and SNNs<sup>10,11</sup>. The novel

407 contribution from this study is that the data intensive process of interleaved training can be  
408 avoided in SNNs by inserting periods of noise-induced spontaneous reactivation – unsupervised  
409 learning – during new task training; similar to how brains undergo offline consolidation periods  
410 during sleep resulting in reduced retroactive interference to previously learned tasks<sup>21,43</sup>. In fact,  
411 our results are in line with previous work done in humans showing that perceptual learning tasks  
412 are subject to retroactive interference by competing memories without an intervening period of  
413 REM sleep<sup>37,38</sup>. Moreover, performance on visual discrimination tasks in particular have been  
414 shown to steadily improve over successive nights of sleep<sup>38</sup>, consistent with our findings that  
415 interleaving multiple periods of sleep with novel task learning leads to optimal performance on  
416 each task.

417         Our study predicts synaptic level mechanisms of how sleep-based memory reactivation  
418 can protect old memory traces during training of a new interfering memory task. It suggests the  
419 apparent loss of recall performance for older tasks in ANNs and SNNs after new training does  
420 not necessarily imply a complete erasure of the old task, but instead indicates that the old tasks  
421 decision states became unreachable by the associated inputs. Sleep can reverse the damage to  
422 synaptic connectivity by replaying the old memory traces without explicit usage of the old  
423 training data.

424

## 425 **Methods**

426 **Environment.** Foraging behavior took place in a virtual environment consisting of a 50x50 grid  
427 with randomly distributed “food” particles. Each particle was two pixels in length and could be  
428 classified into one of four types depending on its orientation: vertical, horizontal, positively

429 sloped diagonal, or negatively sloped diagonal. During the initial unsupervised training period,  
430 the particles are distributed at random with the constraints that each of the four types are equally  
431 represented and no two particles can be directly adjacent. During training and testing periods  
432 only the task-relevant particles were present. When a particle was acquired as a result of the  
433 virtual agent moving, it was removed from its current location (simulating consumption) and  
434 randomly assigned to a new location on the grid, again with the constraint that it not be directly  
435 adjacent to another particle. This ensures a continuously changing environment with a constant  
436 particle density. The density of particles in the environment was set to 10%. The virtual agent  
437 can see a 7x7 grid of squares (the “visual field”) centered on its current location and it could  
438 move to any adjacent square, including diagonally, for a total of eight directions.

439

440 **Network structure.** The network was composed of 842 spiking map-based neurons (see  
441 *Methods: Map-based neuron model* below)<sup>50,51</sup>, arranged into three feed-forward layers to  
442 mimic a basic biological circuit: a 7x7 input layer (I), a 28x28 hidden layer (H), and a 3x3 output  
443 layer (O) with a nonfunctional center neuron (Fig 1). Input to the network was simulated as a set  
444 of suprathreshold inputs to the neurons in layer I, equivalent to the lower levels of the visual  
445 system, which represent the position of particles in an egocentric reference frame relative to the  
446 virtual agent (positioned in the center of the 7x7 visual field). The most active neuron in layer O,  
447 playing the role of biological motor cortex, determined the direction of the subsequent  
448 movement. Each neuron in layer H, which can be loosely defined as higher levels of the visual  
449 system or associative cortex, received excitatory synapses from 9 randomly selected neurons in  
450 layer I. These connections initially had random strengths drawn from a normal distribution. Each  
451 neuron in layer H connected to every neuron in layer O with both an excitatory ( $W_{ij}$ ) and an

452 inhibitory ( $WI_{ij}$ ) synapse. This provided an all-to-all connectivity pattern between these two  
453 layers and accomplished a balanced feed-forward inhibition<sup>52</sup> found in many biological  
454 structures<sup>52-57</sup>. Initially, all these connections had uniform strengths and the responses in layer O  
455 were due to the random synaptic variability. Random variability was a property of all synaptic  
456 interactions between neurons and was implemented as variability in the magnitude of the  
457 individual synaptic events.

458

459 **Policy.** Simulation time was divided up into epochs of 600 timesteps, each roughly equivalent to  
460 300 ms. At the start of each epoch the virtual agent received input corresponding to locations of  
461 nearby particles within the 7x7 “visual field”. Thus 48 of the 49 neurons in layer I received input  
462 from a unique location relative to the virtual agent. At the end of the epoch the virtual agent  
463 made a single move based on the activity in layer O. If the virtual agent moved to a grid location  
464 with a “food” particle present, the particle was removed and assigned to a randomly selected new  
465 location.

466 Each epoch was of sufficient duration for the network to receive inputs, propagate  
467 activity forward, produce outputs, and return to a resting state. Neurons in layer I which  
468 represent locations in the visual field containing particles received a brief pulse of excitatory  
469 stimulation sufficient to trigger a spike; this stimulation was applied at the start of each  
470 movement cycle (epoch). At the end of each epoch the virtual agent moved according to the  
471 activity which has occurred in layer O.

472 The activity in layer O controlled the direction of the virtual agent’s movement. Each of  
473 the neurons in layer O mapped onto a specific direction (i.e. one of the eight adjacent locations  
474 or the current location). The neuron in layer O which spiked the greatest number of times during

475 the first half of the epoch defined the direction of movement for that epoch. If there was a tie, the  
476 direction was chosen at random from the set of tied directions. If no neurons in layer O spiked,  
477 the virtual agent continued in the direction it had moved during the previous epoch.

478 There was a 1% chance on every move that the virtual agent would ignore the activity in  
479 layer O and instead move in a random direction. Moreover, for every movement cycle that  
480 passed without the virtual agent acquiring a particle, this probability was increased by 1%. The  
481 random variability promoted exploration vs exploitation dynamics and essentially prevented the  
482 virtual agent from getting stuck in movement patterns corresponding to infinite loops. While  
483 biological systems could utilize various different mechanisms to achieve the same goal, the  
484 method we implemented was efficient and effective for the scope of our study.

485

486 **Neuron models.** For all neurons we used spiking model identical to the model used in <sup>12,13</sup> that  
487 can be described by the following set of difference equations <sup>51,58,59</sup>:

488 
$$V_{n+1} = f_{\alpha}(V_n, I_n + \beta_n),$$

489 
$$I_{n+1} = I_n - \mu(V_n + 1) + \mu\sigma + \mu\sigma_n,$$

490 where  $V_n$  is the membrane potential,  $I_n$  is a slow dynamical variable describing the effects of  
491 slow conductances, and  $n$  is a discrete time-step (0.5 ms). Slow temporal evolution of  $I_n$  was  
492 achieved by using small values of the parameter  $\mu \ll 1$ . Input variables  $\beta_n$  and  $\sigma_n$  were used to  
493 incorporate external current  $I_n^{ext}$  (e.g. background synaptic input):  $\beta_n = \beta^e I_n^{ext}$ ,  $\sigma_n = \sigma^e I_n^{ext}$ .  
494 Parameter values were set to  $\sigma = 0.06$ ,  $\beta^e = 0.133$ ,  $\sigma^e = 1$ , and  $\mu = 0.0005$ . The nonlinearity  $f_{\alpha}(V_n,$   
495  $I_n)$  was defined in the form of the piece-wise continuous function:

496 
$$f_{\alpha}(V_n, I_n) = \begin{cases} \alpha(1 - V_n)^{-1} + I_n, & V_n \leq 0 \\ \alpha + I_n, & 0 < V_n < \alpha + I_n \text{ \& } V_{n-1} \leq 0 \\ -1 & \alpha + I_n \leq V_n \text{ or } V_{n-1} > 0, \end{cases}$$

497 where  $\alpha = 3.65$ .

498 This model is very computationally efficient, and, despite its intrinsic low dimensionality,  
499 produces a rich repertoire of dynamics capable of mimicking the dynamics of Hodgkin-Huxley  
500 type neurons both at the single neuron level and in the context of network dynamics<sup>51,58,60</sup>.

501 To model the synaptic interactions, we used the following piece-wise difference equation:

502 
$$I_{n+1}^{syn} = \gamma I_n^{syn} + \begin{cases} (1 - R + 2XR)g_{syn}/W_j, & spike_{pre} \\ 0, & otherwise, \end{cases}$$

503 Here  $g_{syn}$  is the strength of the synaptic coupling, modulated by the target rate  $W_j$  of receiving  
504 neuron  $j$ . Indices *pre* and *post* stand for the pre- and post-synaptic variables, respectively. The  
505 first condition,  $spike_{pre}$ , is satisfied when the pre-synaptic spikes are generated. Parameter  $\gamma$   
506 controls the relaxation rate of synaptic current after a presynaptic spike is received ( $0 \leq \gamma < 1$ ).  
507 The parameter  $R$  is the coefficient of variability in synaptic release. The standard value of  $R$  is  
508 0.12.  $X$  is a random variable sampled from a uniform distribution with range  $[-1, 1]$ . Parameter  
509  $V_{rp}$  defines the reversal potential and, therefore, the type of synapse (i.e. excitatory or inhibitory).  
510 The term  $(1-R+2XR)$  introduces a variability in synaptic release such that the effect of any  
511 synaptic interaction has an amplitude that is pulled from a uniform distribution with range  $[1-R,$   
512  $1+R]$  multiplied by the average value of the synapse.

513

514 **Synaptic plasticity.** Synaptic plasticity closely followed the rules introduced in<sup>12,13</sup>. A rewarded  
515 STDP rule<sup>24-27</sup> was operated on synapses between layers H and O while a standard STDP rule

516 operated on synapses between layers I and H. A spike in a post-synaptic neuron that directly  
 517 followed a spike in a pre-synaptic neuron created a *pre before post* event while the converse  
 518 created a *post before pre* event. Each new post-synaptic (pre-synaptic) spike was compared to all  
 519 pre-synaptic (post-synaptic) spikes with a time window of 120 iterations.

520 The value of an STDP event (trace) was calculated using the following equation <sup>22,23</sup>:

$$521 \quad p = \frac{-|t_r - t_p|}{T_c},$$

$$522 \quad tr_k = K e^p$$

523 where  $t_r$  and  $t_p$  are the times at which the pre- and post-synaptic spike events occurred  
 524 respectively,  $T_c$  is the time constant and is set to 40 ms, and  $K$  is maximum value of the trace  $tr_k$   
 525 and is set to -0.04 for a *post before pre* event and 0.04 for a *pre before post* event.

526 A trace was immediately applied to synapse between neurons in layers I and H. However,  
 527 for synapses between neurons in layers H and O the traces were stored for 6 epochs after its  
 528 creation before being erased. During storage, a trace had an effect whenever there was a  
 529 rewarding or punishing event. In such a case, the synaptic weights are updated as follows:

$$530 \quad W_{ij} \leftarrow W_{ij} \prod_k^{traces} \left( 1 + \frac{W_{i0}}{W_i} * \Delta_k \right),$$

$$531 \quad \Delta_k = S_{rp} \left( \frac{tr_k}{t - t_k + c} \right) \frac{Sum_{tr}}{Avg_{tr}},$$

$$532 \quad Sum_{tr} = \sum_k^{traces} \frac{tr_k}{t - t_k + c},$$

$$533 \quad Avg_{tr} \leftarrow (1 - \delta) Avg_{tr} + \delta Sum_{tr},$$



534 where  $t$  is the current timestep,  $S_{rp}$  is a scaling factor for reward/punishment,  $tr_k$  is the magnitude  
535 of the trace,  $t_k$  is the time of the trace event,  $c$  is a constant (=1 epoch) used for decreasing  
536 sensitivity to very recent spikes,  $W_i = \sum_j W_{ij}$  is the total synaptic strength of all connections from  
537 the neuron  $i$  in layer H to all neurons in layer O,  $W_{i0}$  is a constant that is set to the initial value  
538 (*target value*) of  $W_i$  at the beginning of the simulation. The term  $W_{i0}/W_i$  helped to keep the output  
539 weight sum close to the initial target value. The effect of these rules was that neurons with lower  
540 total output strength could increase their output strength more easily.

541 The network was rewarded when the virtual agent moved to a location which contained a  
542 particle from a “food” pattern (horizontal in Task 1, vertical in Task 2) and  $S_{rp} = 1$ , and received  
543 a punishment of  $S_{rp} = -0.001$  when it moved to a location with a particle from a neutral pattern  
544 (negative/positive diagonal in Task 1/2). A small punishment of  $S_{rp} = -0.0001$  was applied if the  
545 agent moved to a location without a particle present to help the virtual agent learn to acquire  
546 “food” as rapidly as possible. During periods of sleep the network received a constant reward of  
547  $S_{rp} = 0.5$  on each movement cycle.

548 To ensure that neurons in layer O maintained a relatively constant long-term firing rate,  
549 the model incorporated homeostatic synaptic scaling which was applied every epoch. Each  
550 timestep, the total strength of synaptic inputs  $W_j = \sum_i W_{ij}$  to a given neuron in layer O was set  
551 equal to the target synaptic input  $W_{j0}$  – a slow variable which varied over many epochs  
552 depending on the activity of the given neuron in layer O – which was updated according to:

$$553 \quad W_{j0} \leftarrow \begin{cases} W_{j0}(1 + D_{tar}) & \text{spike rate} < \text{target rate} \\ W_{j0}(1 - D_{tar}) & \text{spike rate} > \text{target rate} \end{cases}$$

554 To ensure that the net synaptic input  $W_j$  to any neuron was unaffected by plasticity events  
555 at the individual synapses at distinct timesteps and equal to  $W_{j0}$ , we implemented a scaling

556 process akin to heterosynaptic plasticity which occurs after each STDP event. When any  
557 excitatory synapse of neuron in layer O changed in strength, all other excitatory synapses  
558 received by that neuron were updated according to:

$$559 \quad W_{ij} \leftarrow W_{ij} \frac{W_{j0}}{\sum_i W_{ij}}$$

560

561 **Simulated Sleep.** To simulate the sleep phase, we inactive the sensory receptors (i.e. the input  
562 layer of network), cut off all sensory signals (i.e. remove all particles from the environment), and  
563 decouple output layer activity from motor control (i.e. the output layer can spike but no longer  
564 causes the agent to move). We also change the learning rule between the hidden and output layer  
565 from rewarded to unsupervised STDP (see *Methods: Synaptic Plasticity* for details) as there is no  
566 way to evaluate decision-making without sensory input or motor output.

567 To simulate the spontaneous activity observed during REM sleep, we provided noise to  
568 each neuron in the hidden layer in a way which ensured that the spiking statistics of each neuron  
569 was conserved across awake and sleep phases. To determine these spiking rates, we recorded  
570 average spiking rates of neurons in the hidden layer H during preceding training of both Task 1  
571 and Task 2; these task specific spiking rates were then averaged to generate target spiking rates  
572 for hidden layer neurons. Interleaved<sub>S,T1</sub> training consisted of alternating intervals of this sleep  
573 phase and training on Task 1, with each interval lasting 100 movement cycles (although no  
574 movement occurred).

575

576 **Support Vector Machine Training.** A support vector machine with a radial basis function  
577 kernel was trained to classify synaptic weight configurations as being related to Task 1 or Task

578 2. Labeled training data were obtained by taking the excitatory synaptic weight matrices between  
579 the hidden and output layers from the last fifth of the Task 1 and Task 2 training phases (i.e. after  
580 performance had appeared to asymptote). These synaptic weight matrices were then flattened  
581 into column vectors, and the column vectors were concatenated to form a training data matrix of  
582 size *number of features* x *number of samples*. The number of features was equal to the total  
583 number of excitatory synapses between the hidden and output layer – 6272 dimensions. We then  
584 used this support vector machine to classify held out synaptic weight configurations from Task 1  
585 and Task 2 training, as well as ones which resulted from Interleaved<sub>T1,T2</sub> and Interleaved<sub>S,T1</sub>  
586 training.

587

588 **2-D Synaptic Weight distributions (Figure 6).** First for each synapse we found how its  
589 synaptic strength changes between two slices in time, where the given synapse's strength at time  
590 slice 1 is the point's X-value and strength at time slice 2 is its Y-value. Then we binned this  
591 space and counted synapses in each bin to make two dimensional histograms where blue color  
592 corresponds to a single synapse found in a bin and brown corresponds to the max of 50 synapses.  
593 These two-dimensional histograms assist in visualizing the movement of all synapses between  
594 the two slices in time that are specified by the timelines at the top of each plot. Conceptually, it is  
595 important to note that if a synapse does not change in strength between time slice 1 and time  
596 slice 2, then point the synapse corresponds to in this space will lie on the diagonal of the plot  
597 since the X-value will match the Y-value. If a great change in the synapse's strength has  
598 occurred between time slice 1 and time slice 2, then the synapse's corresponding point will lie  
599 far from the diagonal since the X-value will be distant from the Y-value. The points on the X-

600 (Y-) axis represent synapses that lost (gained) all synaptic strength between time slice 1 and time  
601 slice 2.

602

603 **Distance from Solution Manifolds (Figure 7).** Each of the two solution manifolds (i.e. Task 1  
604 and Task 2 specific manifolds) were defined by the point-sets in synaptic weight space which  
605 were capable of supporting robust performance on that particular task, namely the sets  $M_{T1}$  and  
606  $M_{T2}$ . This included the synaptic weight states from the last fifth of training on a particular task  
607 (i.e. after performance on that task appeared to asymptote) and all of the synaptic weight states  
608 from the last fifth of both Interleaved<sub>T1,T2</sub> and Interleaved<sub>S,T1/T2</sub> training. The intersection of the  
609 two solution manifolds (i.e. the point-set  $M_{T1 \cap T2}$ ) was defined solely by the synaptic weight states  
610 from the last fifth of both Interleaved<sub>T1,T2</sub> and Interleaved<sub>S,T1</sub> training. As the network evolved  
611 along its trajectory in synaptic weight space, the distance from the current point in synaptic  
612 weight space,  $p_t$ , to the two solution manifolds and their intersection were computed as follows:

613 
$$d^n(p_t, M_\tau) = \min_{x \in M} (d^n(p_t, x)).$$

614 Here,  $d^n$  is the n-dimensional Euclidean-distance function, where  $n$  is the dimensionality of  
615 synaptic weight space (i.e.  $n = 6272$  here),  $M_\tau$  is the point-set specific to the manifold or  
616 intersection in question (i.e. either  $M_{T1}$ ,  $M_{T2}$ , or  $M_{T1 \cap T2}$ ), and  $x$  is a particular element of the  
617 point-set  $M$ .

618

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626

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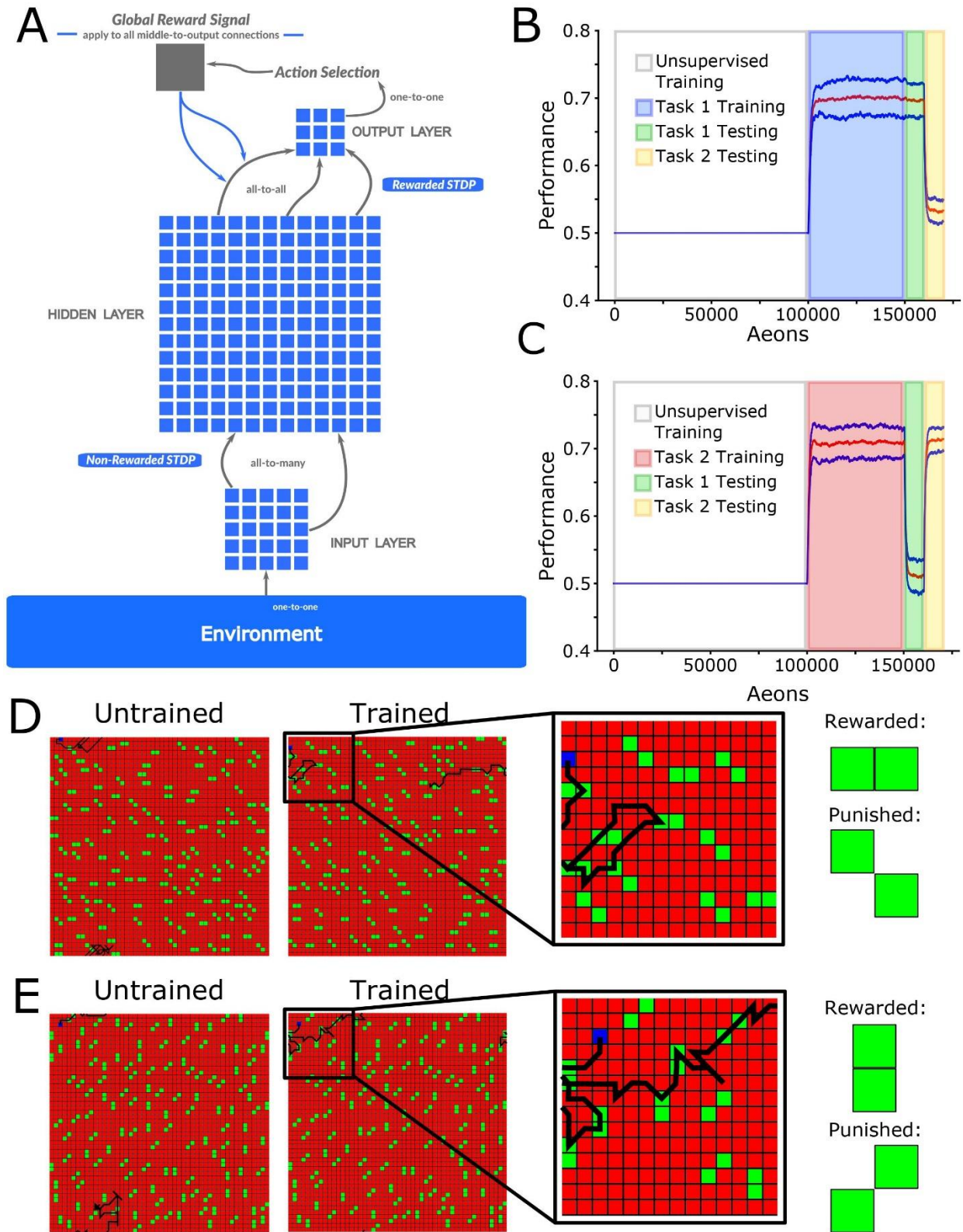
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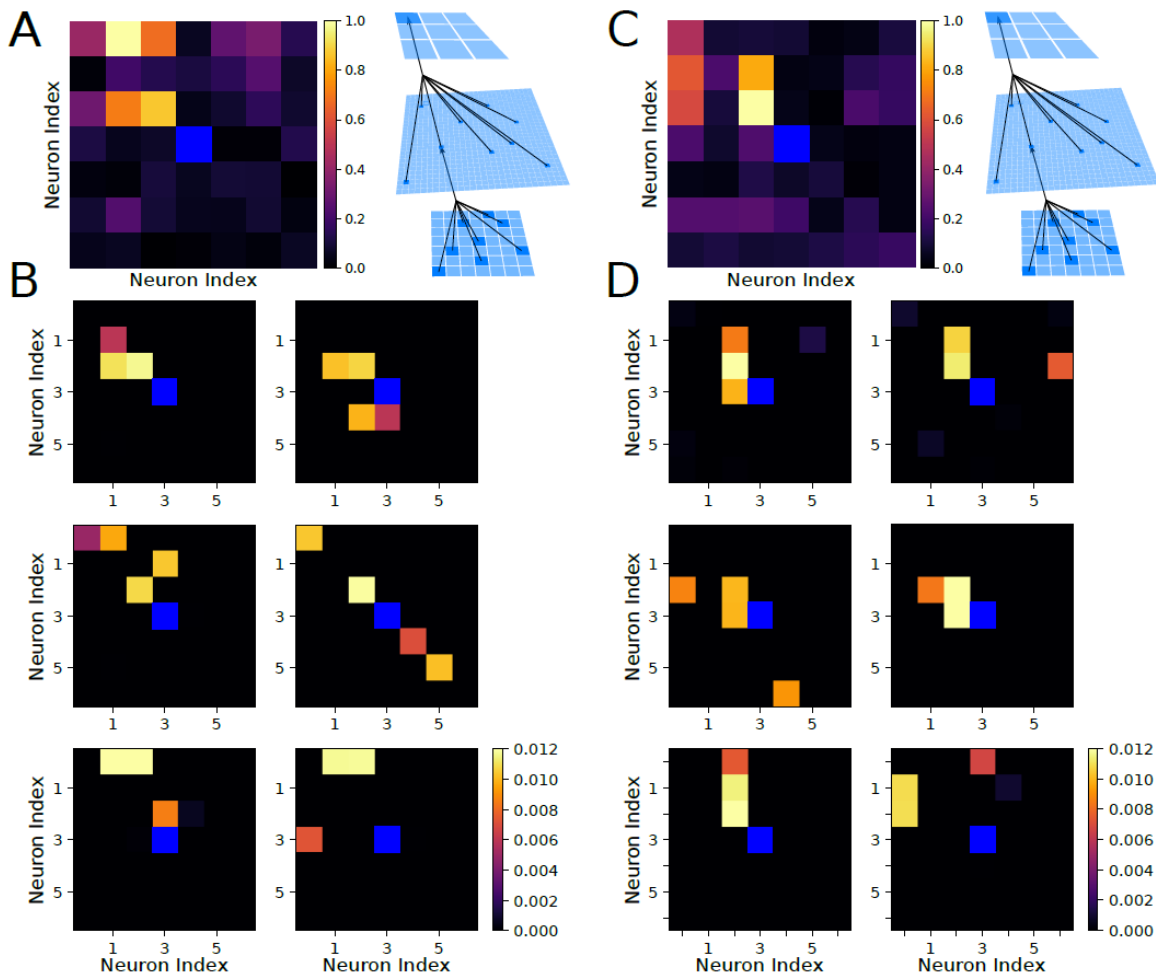


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770 **Figure 1. Network architecture and complementary foraging task structure. (A) The**

771 network had three layers of neurons with a feed-forward connectivity scheme. Input from the  
772 “visual field” (7x7 subspace of 50x50 virtual environment) was simulated as a set of excitatory  
773 inputs to the input layer neurons representing the position of food particles in an egocentric  
774 reference frame relative to the virtual agent. Each hidden layer neuron received an excitatory  
775 synapse from 9 randomly selected input layer neurons. Excitatory synapses between input and  
776 hidden layer neurons were subject to unsupervised STDP, while those between hidden and  
777 output layer neurons were subject to rewarded STDP. Each output layer neuron received one  
778 excitatory and one inhibitory synapse from each hidden layer neuron. The most active neuron in  
779 the output layer (size 3x3) determined the direction of movement. **(B)** Mean performance (red  
780 line) and standard deviation (blue lines) over time: 100,000 aeons (1 aeon = 100 movement  
781 cycles) of unsupervised training (white), 50,000 aeons of Task 1 training (blue), and 10,000  
782 aeons of Task 1 (green) and Task 2 (yellow) testing. The y-axis represents the agent’s  
783 performance, or the probability of acquiring rewarded as opposed to punished particle patterns.  
784 The x-axis is time in aeons. Mean performance during testing on Task 1 was  $0.70 \pm 0.02$  while  
785 Task 2 was  $0.53 \pm 0.02$ . **(C)** The same as shown in (B) except now for: 10,000 aeons of  
786 unsupervised training (white), 5000 aeons of Task 2 training (red), and 1,000 aeons of Task 1  
787 (green) and Task 2 (yellow) testing. Mean performance during testing on Task 1 was  $0.51 \pm 0.02$   
788 while Task 2 was  $0.71 \pm 0.02$ . **(D)** Examples of trajectories through the environment at the  
789 beginning (left) and at the end (middle-left) of training on Task 1, with a zoom in on the  
790 trajectory at the end of training (middle-right), and the values of the task-relevant food particles  
791 (right). **(E)**. The same as shown in (D) except now for Task 2.

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794 **Figure 2. Receptive fields of output and hidden layer neurons determine the agent policy.**

795 **(A)** Left, Receptive field of the output layer neuron controlling movement to the upper-left

796 direction following training on Task 1. This neuron can be seen to selectively respond to

797 horizontal orientations in the upper-left quadrant of the visual field. Right, Schematic of

798 connections between layers. **(B)** Examples of receptive fields of hidden layer neurons which

799 synapse strongly onto the output neuron from (A) after training on Task 1. The majority of these

800 neurons selectively respond to horizontal food particles in the upper-left quadrant of the visual

801 field, with one neuron (middle-right) selectively responding to the presence of negative diagonal

802 food particles in the bottom-right quadrant and the lack of negative diagonal food particles in the

803 upper-left quadrant of the visual field. **(C)** The same as shown in (A) except following training

804 on Task 2. The upper-left decision neuron can be seen to selectively respond to vertical  
805 orientations in the upper-left quadrant of the visual field. **(D)** The same as shown in (B) except  
806 following training on Task 2. All of these neurons selectively respond to vertical food particles in  
807 the upper-left quadrant of the visual field.

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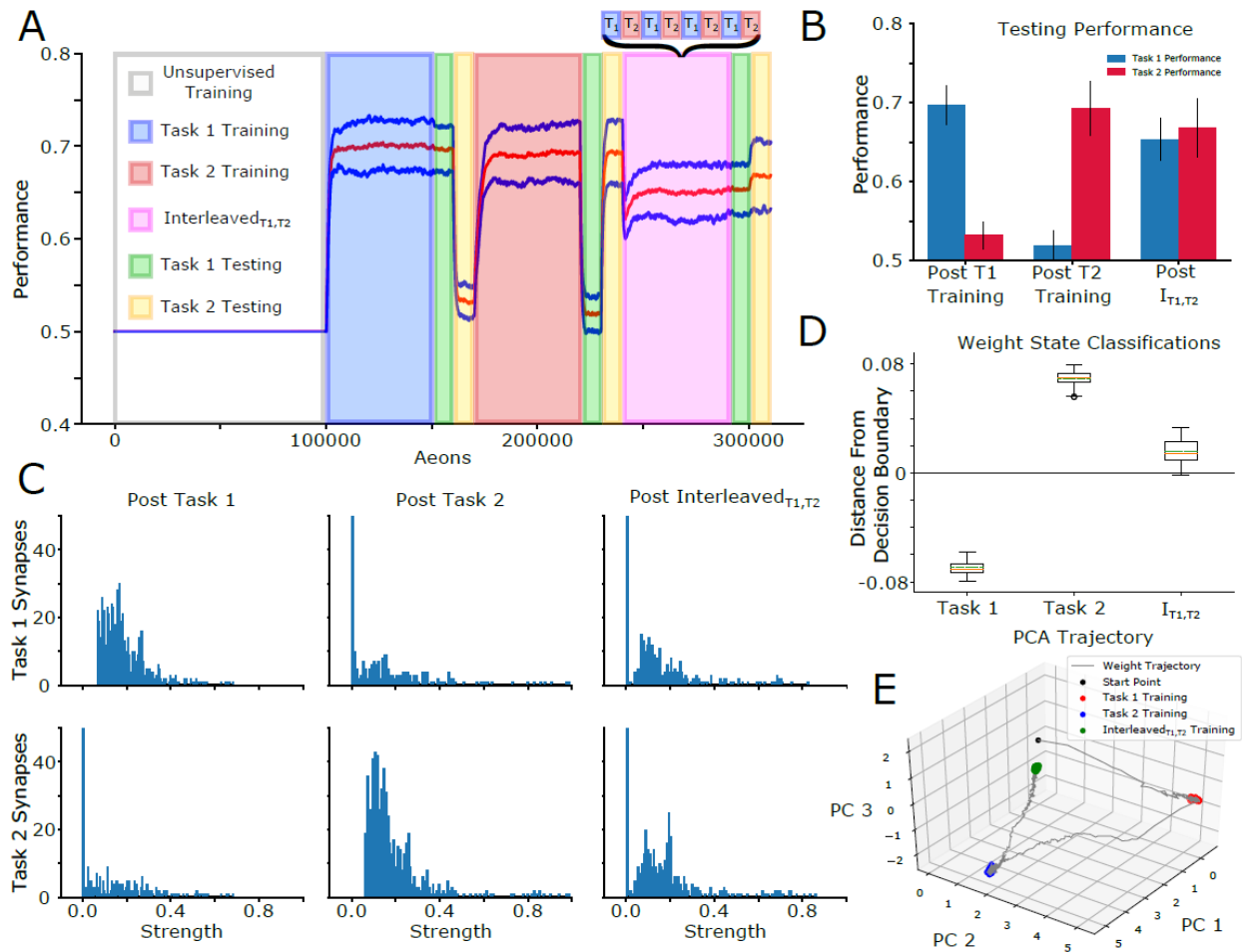
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818 **Figure 3. Sequential training on complementary tasks induces catastrophic forgetting**

819 **which can be rescued by interleaved training. (A)** Mean performance (red line) and standard

820 deviation (blue lines) over time: 100,000 aeons of unsupervised training (white), 50,000 aeons of

821 Task 1 training (blue), 10,000 aeons of Task 1 (green) and Task 2 (yellow) testing, 50,000 aeons

822 of Task 2 training (red), 10,000 aeons of Task 1 (green) and Task 2 (yellow) testing, 50,000

823 aeons of Interleaved<sub>T1,T2</sub> training (purple), 10,000 aeons of Task 1 (green) and Task 2 (yellow)

824 testing. **(B)** Mean and standard deviation of performance during testing on Task 1 (blue) and

825 Task 2 (red) after each training period. Following Task 1 training, mean performance on Task 1

826 was  $0.69 \pm 0.02$  while Task 2 was  $0.53 \pm 0.02$ . Conversely, following Task 2 training, mean

827 performance on Task 1 was  $0.52 \pm 0.02$  while Task 2 was  $0.69 \pm 0.04$ . Following Interleaved<sub>T1,T2</sub>

828 training, mean performance on Task 1 was  $0.65 \pm 0.03$  while Task 2 was  $0.67 \pm 0.04$ . **(C)**

829 Distributions of task-relevant synaptic weights. The distributional structure of Task 1-relevant

830 synapses following Task 1 training (top-left) is destroyed following Task 2 training (top-middle),

831 but partially recovered following Interleaved<sub>T1,T2</sub> training (top-right). Similarly, the distributional

832 structure of Task 2-relevant synapses following Task 2 training (bottom-middle), which was not

833 present following Task 1 training (bottom-left), was partially preserved following

834 Interleaved<sub>T1,T2</sub> training (bottom-right). **(D)** Box plots with mean (dashed green line) and median

835 (dashed orange line) of the distance to the decision boundary found by an SVM trained to

836 classify Task 1 and Task 2 synaptic weight matrices for Task 1, Task 2, and Interleaved<sub>T1,T2</sub>

837 training across trials. Task 1 and Task 2 synaptic weight matrices had mean classification values

838 of -0.069 and 0.069 respectively, while that of Interleaved<sub>T1,T2</sub> training was 0.016. **(E)** Trajectory

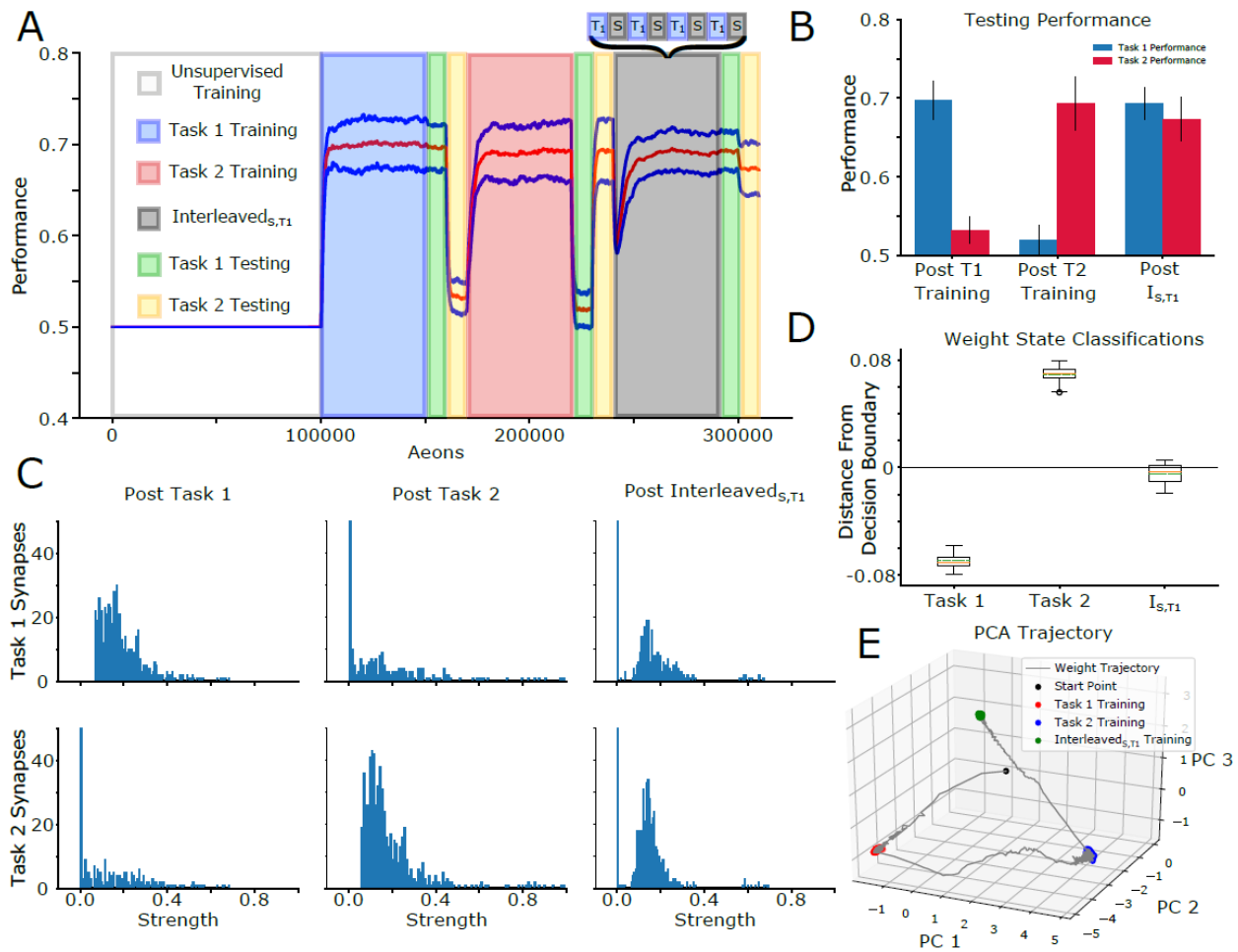
839 of H to O layer synaptic weights through PC space. Synaptic weights which evolved during

840 Interleaved<sub>T1,T2</sub> training (green dots) clustered in a location of PC space intermediary between

841 the clusters of synaptic weights which evolved during training on Task 1 (red dots) and Task 2

842 (blue dots).

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845 **Figure 4. Periods of sleep interleaved with training on a new task can prevent catastrophic**

846 **forgetting. (A)** Task paradigm similar to that shown in (3A) but with 50,000 aeons of

847 Interleaved<sub>S,T1</sub> training (gray) instead of Interleaved<sub>T1,T2</sub> training. Note that performance for Task

848 2 remains high despite no Task 2 training during this period. **(B)** Mean and standard deviation of

849 performance during testing on Task 1 (blue) and Task 2 (red) after each training period.

850 Following Task 1 training, mean performance on Task 1 was  $0.70 \pm 0.02$  while Task 2 was  $0.53$

851  $\pm 0.02$ . Conversely, following Task 2 training, mean performance on Task 1 was  $0.52 \pm 0.02$

852 while Task 2 was  $0.69 \pm 0.04$ . Following Interleaved<sub>S,T1</sub> training, mean performance on Task 1

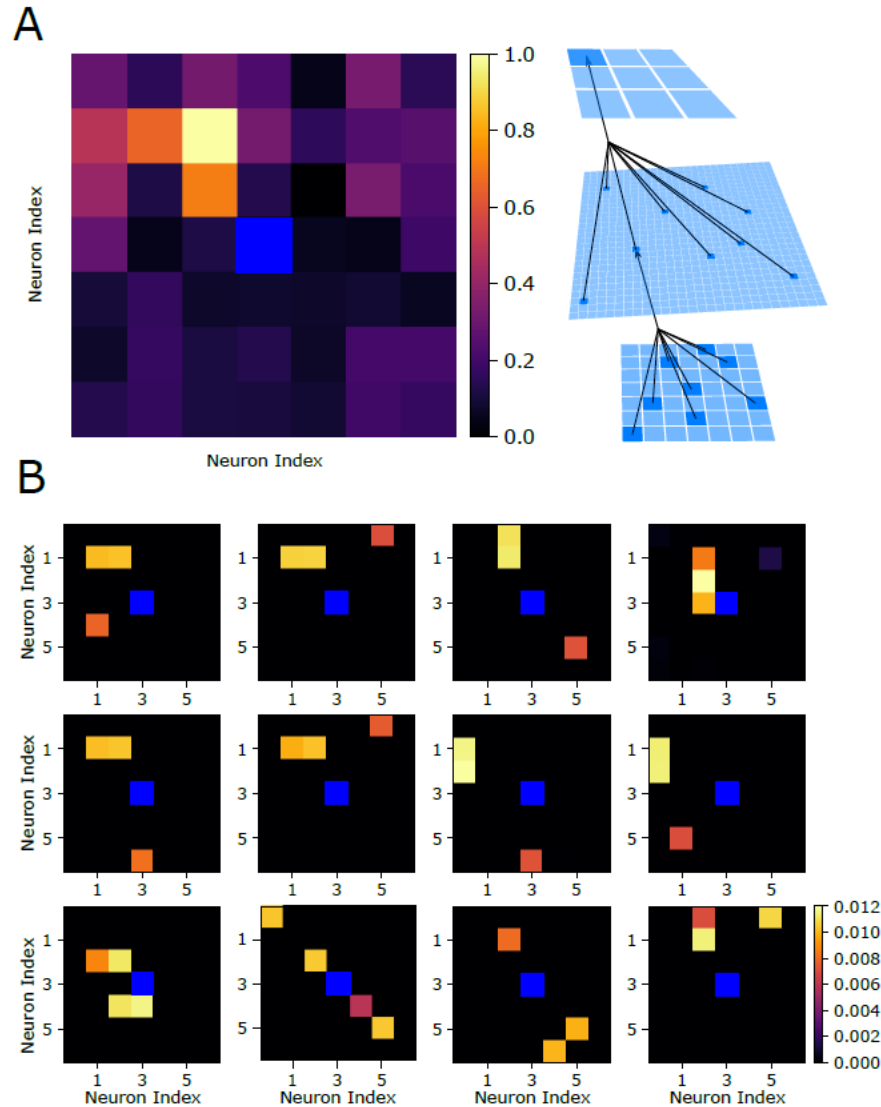
853 was  $0.69 \pm 0.02$  while Task 2 was  $0.67 \pm 0.03$ . **(C)** Distributions of task-relevant synaptic

854 weights. The distributional structure of Task 1-relevant synapses following Task 1 training (top-



855 left) is destroyed following Task 2 training (top-middle), but partially recovered following  
856 Interleaved<sub>S,T1</sub> training (top-right). Similarly, the distributional structure of Task 2-relevant  
857 synapses following Task 2 training (bottom-middle), which was not present following Task 1  
858 training (bottom-left), was partially preserved following Interleaved<sub>S,T1</sub> training (bottom-right).  
859 Task-relevant synapses were considered to be those which had a synaptic weight of at least 0.1  
860 following training on that task. **(B)** Box plots with mean (dashed green line) and median (dashed  
861 orange line) of the distance to the decision boundary found by an SVM trained to classify Task 1  
862 and Task 2 synaptic weight matrices for Task 1, Task 2, and Interleaved<sub>S,T1</sub> training across trials.  
863 Task 1 and Task 2 synaptic weight matrices had mean classification values of -0.069 and 0.069  
864 respectively, while that of Interleaved<sub>S,T1</sub> training was -0.0047. **(C)** Trajectory of H to O layer  
865 synaptic weights through PC space. Synaptic weights which evolved during Interleaved<sub>S,T1</sub>  
866 training (green dots) clustered in a location of PC space intermediary between the clusters of  
867 synaptic weights which evolved during training on Task 1 (red dots) and Task 2 (blue dots).  
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870 **Figure 5. Receptive fields following interleaved Sleep and Task 1 training reveal how the**  
871 **network can multiplex the complementary tasks. (A) Left, Receptive field of the output layer**  
872 **neuron controlling movement to the upper-left direction following interleaved sleep and Task 1**  
873 **training. This neuron has a complex receptive field capable of responding to horizontal and**  
874 **vertical orientations in the upper-left quadrant of the visual field. Right, Schematic of the**  
875 **connectivity between layers. (B) Examples of receptive fields of hidden layer neurons which**  
876 **synapse strongly onto the output neuron from (A) after interleaved Sleep and Task 1 training.**

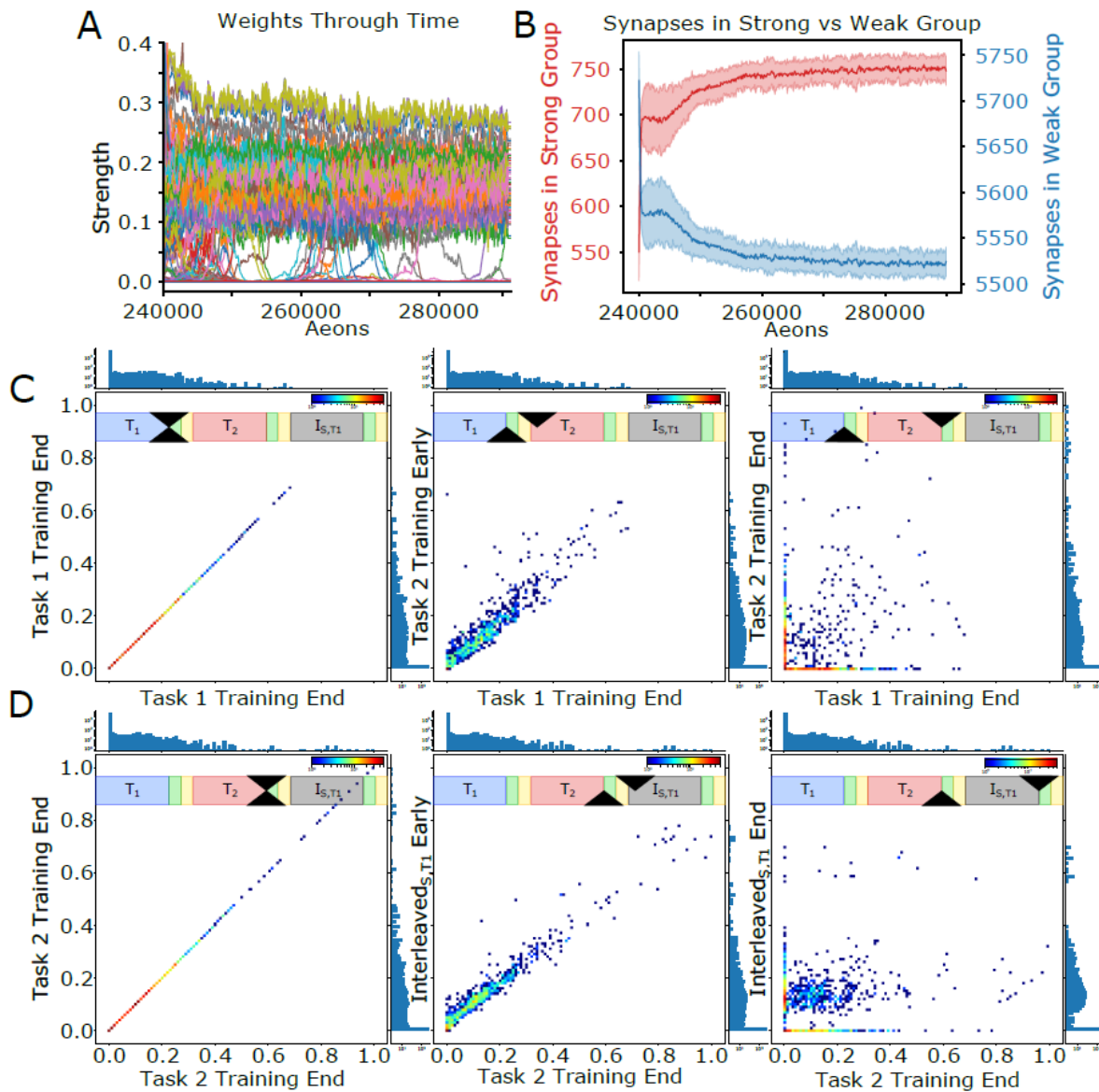
877 The majority of these neurons selectively respond to horizontal food particles (left half) or  
878 vertical food particles (right half) in the upper-left quadrant of the visual field, promoting  
879 movement in that direction and acquisition of the rewarded patters. A few neurons (bottom-  
880 middle-left/right) can be seen to selectively respond to the presence of positive/negative diagonal  
881 food particles in the bottom-right quadrant of the visual field. Activation of these neurons will  
882 promote avoidance movement to the upper-left direction away from the punished patterns.

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888 **Figure 6. Periods of sleep allow learning Task 1 without interference with old Task 2**

889 **through renormalization of task-relevant synapses.** (A) Dynamics of all incoming synapses to

890 a single output layer neuron during  $\text{Interleaved}_{s,T1}$  training shows the synapses separate into two

891 clusters. (B) Number of synapses in the strong (red) and weak (blue) clusters during

892  $\text{Interleaved}_{s,T1}$ . (C) Two-dimensional histograms illustrating synaptic weights dynamics. For

893 each plot, the x-axis represents synaptic weight after Task 1 training and the y-axis represents the

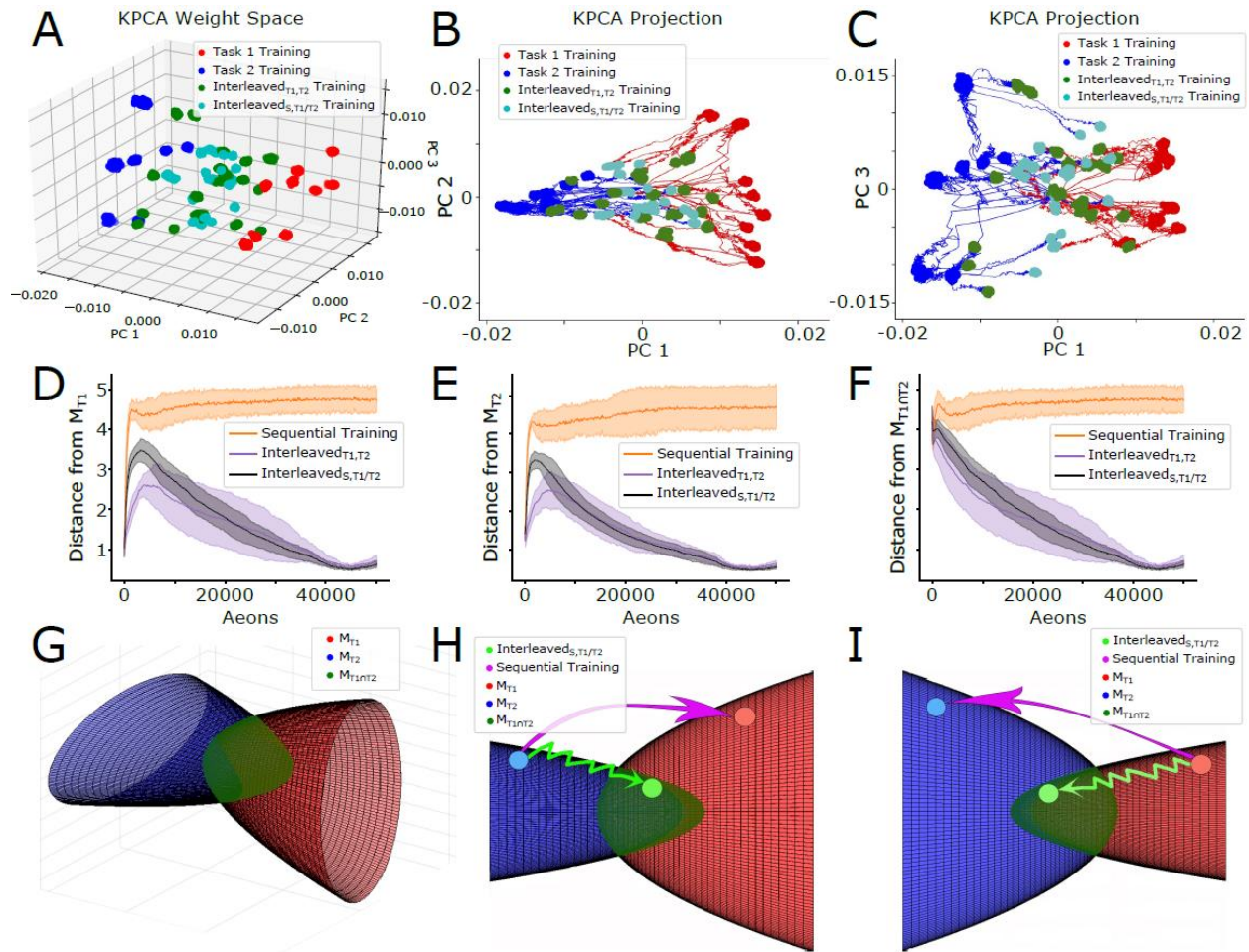
894 synaptic weight at a different point in time (Scale bar: brown - 50 synapses/bin, blue - 1

895 synapse/bin. One-dimensional projections along top and right sides show the global distribution  
896 of synapses at the time slices for a given plot. If no training occurred between the time slices, a  
897 diagonal plot depicts that synaptic weights have not changed (left). After a small amount of Task  
898 2 training, all points lie near the diagonal (middle) indicating minimal changes to synaptic  
899 weights. Once Task 2 is fully trained (right), many synapses move far away from their original  
900 values. In particular, a red cluster along the x-axis indicates synapses which were strong after  
901 Task 1 training but were erased after Task 2 training. **(D)** Same as (C) except the x-axis refers to  
902 the end of Task 2 training. Again, a diagonal plot is attained when no training takes place  
903 between the time slices (left), and points lie near the diagonal when only a small amount of  
904 Interleaved<sub>S,T1</sub> training occurs (middle). After a full period of Interleaved<sub>S,T1</sub> training (right),  
905 weak synapses were recruited to support Task 1 (red cluster along the y-axis) and many Task 2  
906 specific synapses remained moderately strong (blue cluster along x-axis).

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911 **Figure 7. Periods of sleep push the network towards the intersection of Task 1 and Task 2**

912 **specific solution manifolds. (A-C)** Low-dimensional visualizations of the synaptic weight

913 configurations of 10 networks obtained through kPCA for 3-dimensions (A), 2-dimensions using

914 PC 1 and PC 3 (B), and 2-dimensions using PC 1 and PC 3 (C). Synaptic weight configurations

915 taken from the last fifth of Task 1 (red dots), Task 2 (blue dots), Interleaved $_{T1,T2}$  (green dots), and

916 Interleaved $_{S,T1/T2}$  (cyan dots) training are shown. PC 1 characterizes good performance on Task 1

917 (positively valued) or Task 2 (negatively valued) training. PC 2 (PC 3) characterizes the

918 variability in Task 1 (Task 2) training. Trajectories resulting from Interleaved $_{T1,T2}$  and

919 Interleaved $_{S,T1/T2}$  training following Task 1 (Task 2) training are shown in red (blue).

920 Average (solid lines) and standard deviation (shaded regions) of the n-dimensional Euclidean

921 distances between the current synaptic weight configuration and  $M_{T1}$  (D),  $M_{T2}$  (E), and  $M_{T1 \cap T2}$   
922 (F) during Sequential (orange), Interleaved<sub>T1,T2</sub> (purple), and Interleaved<sub>S,T1/T2</sub> (black) training.  
923 Following Task 2 (D) or Task 1 (E) training, Sequential training on the opposite task causes the  
924 synaptic weight configuration to diverge from the initial solution manifold, while Interleaved<sub>T1,T2</sub>  
925 and Interleaved<sub>S,T1/T2</sub> training do not. (F) Interleaved<sub>T1,T2</sub> and Interleaved<sub>S,T1/T2</sub> training cause the  
926 synaptic weight configuration to converge to  $M_{T1 \cap T2}$  while Sequential training avoids this  
927 intersection. (G) Authors' interpretation of the task-specific point-sets shown in (A-C) as  
928 solution manifolds  $M_{T1}$  (red) and  $M_{T2}$  (blue).  $M_{T1}$  and  $M_{T2}$  can be thought of as two oppositely  
929 oriented elliptic paraboloids which intersect orthogonally near the origin ( $M_{T1 \cap T2}$ ; dark green).  
930 (H,I) Sequential training (pink arrow) causes the network to jump from one solution manifold to  
931 the other while avoiding  $M_{T1 \cap T2}$ , while Interleaved<sub>S,T1/T2</sub> training (light green arrow) keep the  
932 network close to the initial solution manifold as it converges towards  $M_{T1 \cap T2}$ .

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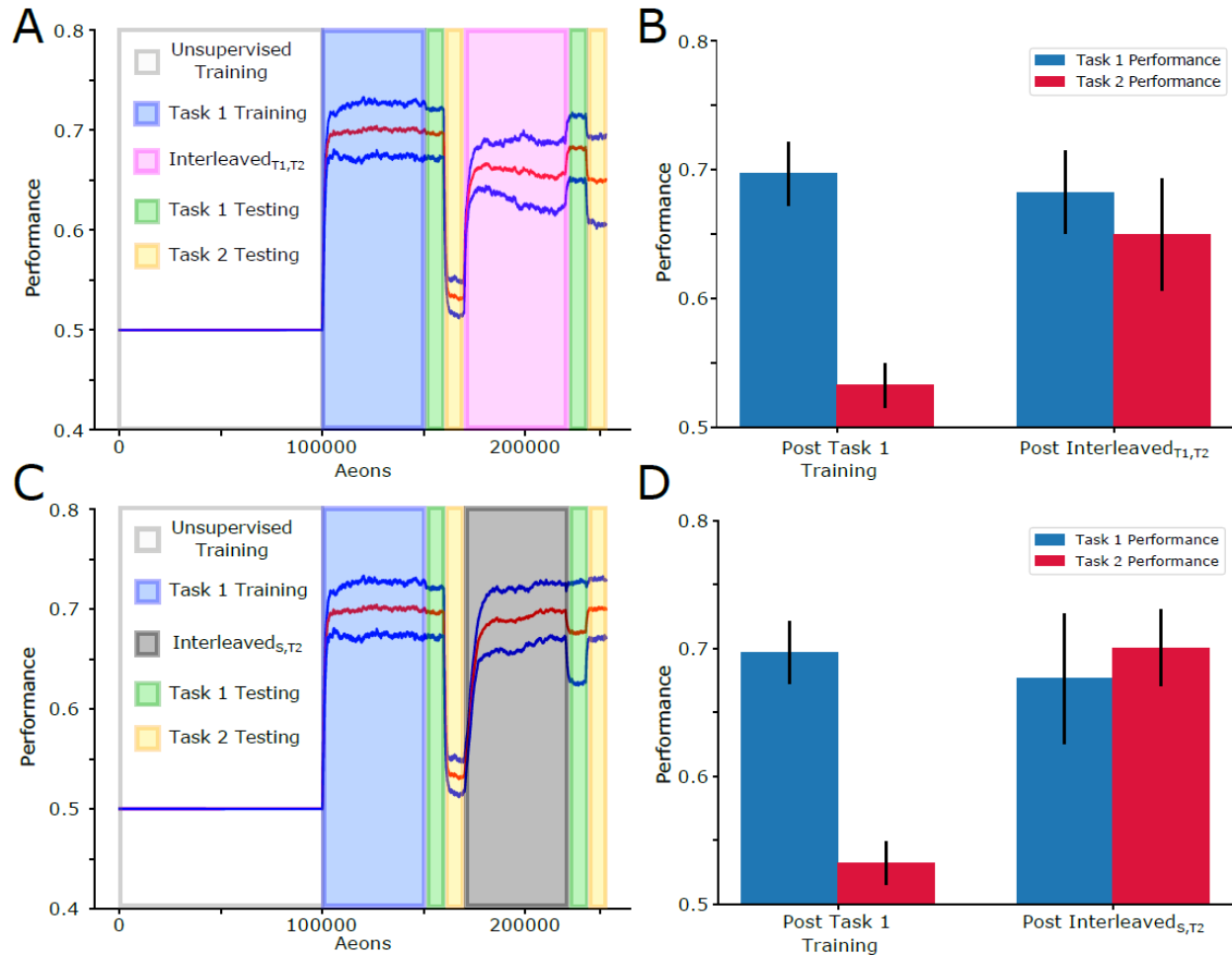
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943 **Extended Data Figure 1. Interleaved training of two tasks and interleaving training new**

944 **task with sleep both can integrate new tasks without catastrophic forgetting. (A). Mean**

945 performance (red line) and standard deviation (blue lines) over time: 100,000 aeons of

946 unsupervised training (white), 50,000 aeons of Task 1 training (blue), 10,000 aeons of Task 1

947 (green) and Task 2 (yellow) testing, 50,000 aeons of Interleaved<sub>T1,T2</sub> training (pink), 10,000

948 aeons of Task 1 (green) and Task 2 (yellow) testing. **(B)** Mean and standard deviation of

949 performance during testing on Task 1 (blue) and Task 2 (red) after each training period.

950 Following Task 1 training, mean performance on Task 1 was  $0.69 \pm 0.02$  while Task 2 was  $0.53$

951  $\pm 0.02$ . Following Interleaved<sub>T1,T2</sub> training, mean performance on Task 1 was  $0.68 \pm 0.03$  while

952 Task 2 was  $0.64 \pm 0.04$ . **(C)** Task paradigm similar to that shown in (A) but with 50,000 aeons of

953 Interleaved<sub>s,T2</sub> training (gray) instead of Interleaved<sub>T1,T2</sub> training. **(D)** Mean and standard

954 deviation of performance during testing on Task 1 (blue) and Task 2 (red) after each training

955 period. Following Task 1 training, mean performance on Task 1 was  $0.70 \pm 0.02$  while Task 2

956 was  $0.53 \pm 0.02$ . Following Interleaved<sub>s,T2</sub> training, mean performance on Task 1 was  $0.68 \pm$   
957  $0.05$  while Task 2 was  $0.70 \pm 0.03$ .

958