

## A neural network account of memory replay and knowledge consolidation

2 Running title: Category replay in deep neural networks

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## Abstract

24 Replay can consolidate memories through offline neural reactivation related to past experiences.  
25 Category knowledge is learned across multiple experiences, and its subsequent generalisation is  
26 promoted by consolidation and replay during rest and sleep. However, aspects of replay are difficult  
27 to determine from neuroimaging studies. We provided insights into category knowledge replay by  
28 simulating these processes in a neural network which approximated the roles of the human ventral  
29 visual stream and hippocampus. Generative replay, akin to imagining new category instances,  
30 facilitated generalisation to new experiences. Consolidation-related replay may therefore help to  
31 prepare us for the future as much as remember the past. Generative replay was more effective in later  
32 network layers functionally similar to the lateral occipital cortex than layers corresponding to early  
33 visual cortex, drawing a distinction between neural replay and its relevance to consolidation. Category  
34 replay was most beneficial for newly acquired knowledge, suggesting replay helps us adapt to changes  
35 in our environment. Finally, we present a novel mechanism for the observation that the brain  
36 selectively consolidates weaker information; a reinforcement learning process in which categories  
37 were replayed according to their contribution to network performance. This reinforces the idea of  
38 consolidation-related replay as an active rather than passive process.

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40 Keywords: consolidation, learning, memory, network, replay

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49 **1. Introduction**

50 **1.1 Memory consolidation-related replay**

51 Memory replay refers to the reactivation of experience-dependent neural activity during resting  
52 periods. First observed in rodent hippocampal cells during sleep (Wilson and McNaughton 1994), the  
53 phenomenon has since been detected in humans during rest (Tambini and Davachi 2013; Hermans et  
54 al. 2017; Schapiro et al. 2018; Liu et al. 2019; Wittkuhn and Schuck 2021), and sleep (Schönauer et al.  
55 2017; Zhang et al. 2018). These investigations have revealed replayed experiences are more likely to  
56 be subsequently remembered, therefore replay has been proposed to strengthen the associated  
57 neural connections and to protect memories from being forgotten. This memory consolidation-related  
58 replay can be viewed as distinct from task-related replay, the neural reactivation observed during task  
59 performance which supports cognitive processes such as memory recall (Jafarpour et al. 2014;  
60 Michelmann et al. 2019; Wimmer et al. 2020), visual understanding (Schwartenbeck et al. 2021),  
61 decision making (Liu et al. 2021), planning (Momennejad et al. 2018) and prediction (Ekman et al.  
62 2017). While traditional perspectives view memory consolidation as a gradual process of fixation  
63 whereby memories are stabilised (Squire and Alvarez 1995; McGaugh 2000), in this paper we advocate  
64 the more contemporary view that offline consolidation-related replay is more dynamic in nature  
65 (Mattar and Daw 2018). Using a computational approach, we test hypotheses that offline replay may  
66 be a creative process to serve future goals, that it matters exactly where in the brain replay occurs,  
67 that it helps us at particular stages of learning, and that the brain might actively choose the optimal  
68 experiences to replay.

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70 **1.2 Generative replay of category knowledge**

71 Neural replay which supports memory consolidation during rest and sleep has been traditionally  
72 assumed to be veridical, such that we commit the events of that day to long-term memory by replaying  
73 the episodes as they were originally experienced. However, there are circumstances in which this may  
74 be suboptimal or impractical. For example, a desirable outcome of category knowledge consolidation

75 is to generalise to new experiences rather than recognise past instances. This phenomenon has been  
76 observed after sleep in infants (Gómez et al. 2006; Friedrich et al. 2015; Horváth et al. 2016), and in  
77 adults (Lau et al. 2011). Sleep also recovers the generalisation of phonological categories (Fenn et al.  
78 2003), preserves generalisation performance in perceptual category learning (Graveline and Wamsley  
79 2017), and assists in the abstraction of gist-like prototype representations (Lutz et al. 2017). It is still  
80 not understood how the brain consolidates and replays memory in the service of generalisation. In  
81 addition, although sleep benefits category learning for a limited number of well-controlled  
82 experimental stimuli (Schapiro et al. 2017), in the real world category learning takes place over many  
83 thousands of experiences, and storing each individual experience for replay is an impractical  
84 proposition. For these reasons, we propose the replay of novel, prototypical category instances would  
85 be a more efficient and effective solution. In fact, given the role of the hippocampus in both replay  
86 (Zhang et al. 2018) and the generation of prototypical concepts (Hassabis et al. 2007), we consider this  
87 the most likely form of category replay. While evidence for such generative replay of category  
88 knowledge has yet to be discovered in the human brain, replay of sequences immediately following  
89 task performance in humans has been shown to be flexible, in that items can be re-ordered based on  
90 previously learned rules (Liu et al. 2019). This is reminiscent of “pre-play” observed during task  
91 performance in rodents, where hippocampal “place cells” observed to fire in specific locations  
92 reactivate in a different order to represent a route which has not been taken before (Gupta et al.  
93 2010).

94 Drawing inspiration from these observations, here we test the idea that replay which  
95 facilitates memory consolidation, occurring over extended offline time periods including sleep, might  
96 also be generative in nature, and that it’s flexibility may not just apply to the reorganisation of learned  
97 sequences, but the creation of entirely new instances of a category. While decoding the re-ordering  
98 of stimuli or route knowledge from brain data during replay has been shown to be a tractable  
99 approach, detecting entirely new instances of complex categories from the brain represents a  
100 significant challenge, and has yet to be demonstrated.

101 One approach to address this question is to simulate these processes in an artificial neural  
102 network. Prior research with artificial neural networks has modelled the replay of generated image  
103 stimuli (van de Ven et al. 2020). While revealing a promising avenue of investigation, the results of  
104 this study cannot be easily extrapolated to the brain or human visual experience. For example, the  
105 structure of only five convolutional layers in the network employed represents just a fraction of the  
106 size of larger models which have been shown to extract visual representations similar in nature to  
107 those processed by the brain (Schrimpf et al. 2018), whose complex structure can be compared to the  
108 ventral visual stream processing pathway, indicating a possible correspondence in functional  
109 architecture (Khaligh-Razavi and Kriegeskorte 2014; Güçlü and van Gerven 2015; Devereux et al.  
110 2018), and whose object recognition performance approaches that of humans (He et al. 2015).  
111 Further, the networks employed by van de Ven et al. (2020) had limited visual experience, having been  
112 pre-trained on just 10 categories of objects. In contrast, an adult human brain will harbour a lifetime  
113 of visual knowledge which facilitates the learning of novel concepts. Therefore, to simulate the  
114 learning and generative replay of new categories realistically in adults, using an experienced network  
115 which contains a pre-existing vast body of knowledge about a range of other categories is an essential  
116 starting point. Another feature of the aforementioned study which limits the comparison to humans,  
117 is that the stimuli used were low-resolution photographs measuring 32 x 32 pixels, which do not reflect  
118 the complexity of human visual experience. To accurately simulate human learning and replay, much  
119 larger, high-resolution images which go some way towards approaching the complexity and richness  
120 of everyday human visual experience are required as training stimuli. Finally, prior attempts at replay  
121 in neural networks, whether generative (Kemker and Kanan 2017; van de Ven et al. 2020) or veridical  
122 (Hayes et al. 2021) have been deployed to address the “catastrophic forgetting” problem; the  
123 tendency of artificial networks to forget old categories when new ones are learned (Robins 1995;  
124 French 1999). While this has been proposed as a potential mechanism for why biological agents do  
125 not suffer from catastrophic forgetting, empirical evidence in support of this hypothesis has not been  
126 forthcoming to date. In addition, other solutions have been put forward on how brains and models

127 may avoid catastrophic interference, such as Adaptive Resonance Theory (Grossberg 2013), and elastic  
128 weight consolidation (Kirkpatrick et al. 2017).

129 In this study, we investigated whether offline generative replay of novel concepts facilitated  
130 subsequent generalisation to new experiences using models which attempt to simulate the human  
131 brain and approximate more closely the visual environment in which it learns. To do this, we  
132 implemented generative replay in a well-studied deep convolutional neural network (DCNN), which  
133 consists of a complex architecture organised into five blocks of convolutional layers and boasts a high  
134 “brain-score” indicating the representations it extracts bear a similarity to those extracted by the brain  
135 and it performs favourably to humans in a categorisation task (Schrimpf et al. 2018). The network had  
136 prior experience of learning 1000 diverse categories of objects from over a million high-resolution  
137 complex naturalistic images, a process which is the network equivalent of a lifetime of visual  
138 experience and which yields within the model an optimised, high-functioning visual system. We tasked  
139 the model with learning 10 novel categories it had not seen before, using similarly high-resolution  
140 naturalistic images to those it has seen before, with an average resolution of around 400 x 350 pixels  
141 (Deng et al. 2009), representing an approximate 140-fold increase in visual details from stimuli used  
142 in prior work. The analogue in humans would be coming across 10 new categories we had not seen  
143 before and using our lifelong experience in processing visual information to extrapolate the relevant  
144 identifying features. After learning periods, we then simulated generative replay in the network, which  
145 attempted to mimic human consolidation during sleep, and monitored the network’s performance  
146 when it “woke up” the next day, to ascertain if we could provide computational support for the theory  
147 that such a process underlies the overnight improvements in generalisation observed in humans.

148

### 149 **1.3 Effective neural loci of replay**

150 Another outstanding question regarding replay, is despite being associated with subsequent memory  
151 (Zhang et al. 2018), it is not clear where in the brain replay makes a demonstrable contribution  
152 towards generalisation. Replay has been observed throughout the brain, early in the ventral visual

153 stream (Ji and Wilson 2007; Deuker et al. 2013; Wittkuhn and Schuck 2021), in the ventral temporal  
154 cortex (Tambini et al. 2010; de Voogd et al. 2016), the medial temporal lobe (Staresina et al. 2013;  
155 Schapiro et al. 2018) the amygdala, (Girardeau et al. 2017; Hermans et al. 2017), motor cortex  
156 (Eichenlaub et al. 2020) and prefrontal cortex (Peyrache et al. 2009). It is not known if replay in lower-  
157 level brain regions actually contributes to the observed memory improvements or whether the key  
158 neural changes are made in more advanced areas, and this question cannot be answered using current  
159 neuroimaging approaches. One prior study has implemented replay within an artificial neural network  
160 from a single location at the end of the network (van de Ven et al. 2020). However, because the  
161 compact architecture of this network did not have a clear functional correspondence with information  
162 processing pathways in the brain, and because replay from other locations within the network was  
163 not also implemented for comparison, it is difficult to yield predictions from these results regarding  
164 effective replay locations in the human brain. In the current study, because we simulated replay in a  
165 neural network which processes images in a manner reflective of the human ventral visual stream, we  
166 could compare the effectiveness of replay from different layers with a purported representational  
167 correspondence to specific regions in the brain. In doing so, we aimed to make predictions about the  
168 effective cortical targets of offline memory consolidation in humans.

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#### 170 **1.4 A time-dependent role for replay**

171 Another open question regarding human replay is the duration of its involvement throughout the  
172 learning of novel concepts. It can take humans years to learn and consolidate semantic or conceptual  
173 knowledge (Manns et al. 2003), but neuroimaging studies of replay are limited to a time-span of a day  
174 or two, therefore it is still not known how long replay contributes to this process. Humans are thought  
175 to “reconsolidate” information every time it is retrieved (Dudai 2012), suggesting replay might play a  
176 continual role in the lifespan of memory. However recordings in rodents have shown that replay  
177 diminishes with repeated exposure to an environment over multiple days (Giri et al. 2019), suggesting  
178 the brain may only replay recently learned, vulnerable information. Answering this question in

179 humans remains a challenge because of the impracticalities of tracking replay events for extended  
180 periods. Simulation in a human-like neural network represents a possible alternative to predict the  
181 relative contribution of replay to consolidation over long time-periods, an approach which has not  
182 been attempted to date. Here, we interleaved daily learning with nights of offline replay in a neural  
183 network which simulates the brain to understand at what stage in learning replay may be most  
184 effective in humans.

185

### 186 **1.5 Replay of weakly-learned knowledge**

187 An additional poorly understood principle of replay which we investigated in this study is why  
188 consolidation tends to selectively benefit weakly-learned over well-learned information (Kuriyama et  
189 al. 2004; Drosopoulos et al. 2007; McDevitt et al. 2015; Schapiro et al. 2018). Here, we modelled a  
190 candidate mechanism for how this occurs in the brain, by adding an auxiliary model (theoretically  
191 analogous to the hippocampus) to the neocortical-like model, which could autonomously learn the  
192 best consolidation strategy, determining what to replay and when.

193

### 194 **1.6 Hypotheses**

195 In addressing these outstanding questions regarding replay in the brain, we made a number of  
196 predictions. Because earlier brain regions are thought to extract equivalent basic features from all  
197 categories, we predicted replay of experience would be more effective in promoting learning at  
198 advanced stages of the network. We hypothesised the replay of “imagined” prototypical replay events  
199 would be as effective as veridical replay in helping us to generalise to new, unseen experiences, thus  
200 supporting our conceptualization of replay as a creative process. We predicted that the benefits of  
201 replay may be confined to early in the learning curve when novel category knowledge is being  
202 acquired. Finally, we hypothesised that a dynamic interaction between hippocampal and neocortical-  
203 like models would result in the prioritisation of weakly-learned items, in line with behavioural studies  
204 of memory consolidation.

205 **2. Materials and Methods**

206 **2.1 Neural network**

207 To simulate the learning of novel concepts in the brain, and test a number of hypotheses regarding  
208 replay, we trained a DCNN on 10 new categories of images. The neural network was VGG-16  
209 (Simonyan and Zisserman 2014). This network is trained on a vast dataset of 1.3 million high-resolution  
210 complex naturalistic photographs known as the ImageNet database (Deng et al. 2009), which contains  
211 recognisable objects from 1000 categories in different contexts. The network learns to associate the  
212 visual features of an object with its category label, until it can recognise examples of that object which  
213 it has never seen before, simulating the human ability to generalise prior knowledge to new situations.  
214 The network takes a photograph's pixels as input, and sequentially transforms this input into more  
215 abstract features. It learns to perform these transformations by adjusting 138,357,544 connection  
216 weights across many layers. Its convolutional architecture reduces the number of possible training  
217 weights by searching for informative features in any area of the photographs.

218 In these experiments, we task the VGG-16 network with learning 10 new categories of images.  
219 To do this, we retained the pre-trained "base" of this network, which consisted of 19 layers, organised  
220 into five convolutional blocks. Within each block there were convolutional layers and a pooling layer,  
221 with nonlinear activation functions. To this base, we attached two fully connected layers, each  
222 followed by a "dropout" layer, which randomly zeroed out 50% of units to prevent overfitting to the  
223 training set (Srivastava et al. 2014). At the end of the network a SoftMax layer was attached, which  
224 contained just 10 outputs rather than the original 1000, and predicted which of 10 classes an image  
225 belonged to. To facilitate the learning of 10 new classes, the weights of layers attached to the pre-  
226 trained base were randomly initialised. All model parameters were free to be trained. In total, 10 new  
227 models were trained, each learning 10 new and different classes.

228

229 **2.2 Stimuli**

230 Photographic stimuli for new classes were drawn randomly from the larger ImageNet 2011 fall  
231 database (Russakovsky et al. 2015), and were screened manually by the experimenter to exclude  
232 classes which bore a close resemblance to classes which VGG-16 was originally trained on. In total,  
233 100 new classes were selected, and randomly assigned to the 10 different models to be trained. Within  
234 each class, a set of 1,170 training images, 130 validation images, and 50 test images were selected.  
235 The list of the selected classes is available in Supplementary Table 1.

236

237 **2.3 Baseline training**

238 We first trained a model without implementing replay, to serve as a baseline measure of network  
239 performance, and compare with other conditions which implemented replay. Ten models were  
240 trained on 10 new and different classes. To further prevent overfitting to the training set, images were  
241 augmented before each training epoch. This is similar to a human viewing an object at different  
242 locations, or from different angles, and facilitates the extraction of useful features rather than rote  
243 memorisation of experience. Augmentation could include up to 20-degree rotation, 20% vertical or  
244 horizontal shifting, 20% zoom, and horizontal flipping. Any blank portions of the image following  
245 augmentation were filled with a reflection of the existing image. Images were then pre-processed in  
246 accordance with Simonyan and Zisserman (2014). Depending on the experiment, the network was  
247 trained for 10 or 30 epochs. We used the Adam optimiser (Kingma and Ba 2014) with a learning rate  
248 of 0.0003. A small learning rate was chosen to reflect the fact that learning new categories in an adult  
249 human reflects a “fine-tuning” of an already highly-trained visual system. The training batch size was  
250 set to 36. The training objective was to minimise the categorical cross-entropy loss over the 10 classes.  
251 Training parameters were optimised based on validation set performance. We report the model’s  
252 performance metrics from the test set only. This is a collection of novel images from each category  
253 which the network does not learn nor is it tuned on, therefore reflecting the model’s ability to  
254 generalise to new stimuli after training, and is thus termed “generalisation performance” in the  
255 figures. Training was performed using TensorFlow version 2.2.

256 **2.4 Replay**

257 Replay was conducted between training epochs, to simulate “days” of learning and “nights” of offline  
258 consolidation. We conceptualised replay representations as generative, in other words they  
259 represented a prototype of that category never seen before, from a particular point in the network.  
260 To generate these representations, the network activations induced by the training images from the  
261 preceding epoch were extracted from a particular layer in the network using the Keract toolbox (Remy  
262 2020). For each class separately, a multivariate distribution of activity was created from these  
263 activations using the SciPy toolbox (<https://scipy.org/>). This multivariate normal distribution is an  
264 extension of the one-dimensional normal distribution to higher dimensions, and is specified by its  
265 mean and covariance matrix. This resulted in a single unique distribution for each specific class, which  
266 represented the relationship between units of the layer which had been previously observed for that  
267 class. We then sampled randomly from this distribution, creating novel activation patterns for that  
268 class at that point in the network (Fig 1A). These novel activation patterns represented a prototype of  
269 that category. The end result was a representation that was a rough approximation of the layer’s  
270 representations of that category if a real image was processed, but novel in nature (see supplementary  
271 Fig 1). The human brain equivalent would be the approximate pattern of neural activity which is  
272 representative of that category at a particular stage in the ventral visual stream. In the brain, these  
273 hypothetical prototypical concepts would be likely generated from more high-level regions such as  
274 the hippocampus and prefrontal cortex (Hassabis et al. 2007; Bowman et al. 2020). Our model was  
275 generative as it could create new samples, however it offered several advantages over traditional  
276 generative models. We were not limited by a bottleneck symmetrical architecture, and our procedure  
277 allowed the model to learn generative samples at multiple levels of representation. Further, our model  
278 represented a proper vision model which showed parallels with the functional architecture of the  
279 ventral visual stream in the brain, whereas current generative models do not show this  
280 correspondence or scale well to such a deep architecture. Finally, our model is specialised for object  
281 recognition, with the resulting generated representations shaped by these task pressures.

282 The number of novel representations created for replay was equivalent to the number of  
283 original training images (1,170). To test where in the network replay is most effective, this process was  
284 performed at one of five different network locations, namely the max pooling layers at the end of each  
285 block (Fig 1A). For the first four pooling layers, creating a multivariate distribution from such a large  
286 number of units was computationally intractable, therefore activations for each filter in these layers  
287 were first down-sampled by a factor of eight for layer one, by four for layers two and three and two  
288 for layer four. The samples drawn from the resulting distribution were then up-sampled back to their  
289 original resolution. These lower-resolution samples are also theoretically relevant, in that they were  
290 created to mimic the schematic nature of mental and dream imagery which takes place during rest  
291 and sleep. To replay these samples through the network, the VGG-16 network was temporarily  
292 disconnected at the layer where replay was implemented, and a new input layer was attached which  
293 matched the dimensions of the replay representations. This truncated network was trained on the  
294 replay samples using the same parameters as regular training. We assume that the brain actively  
295 chooses to replay each concept learned that day, by reactivating the prototypical representations  
296 extracted from many experiences and the associated category label together during sleep. After each  
297 epoch of replay training, the replay section of the network was reattached to the original base, and  
298 training on real images through the whole network resumed. To assess the effects of generative replay  
299 on stimuli disambiguation, we took 10 classes from the 100 which were highly similar (plants, see  
300 supplementary table 2), and trained an additional network on these categories. We then assessed  
301 whether replaying similar classes in the same model led to a greater relative increase in class  
302 performance from baseline accuracies. We did this by dividing the increase in generalisation  
303 performance resulting from replay by the original baseline performance. To find out how many  
304 exemplars are needed for generative replay to have a beneficial effect on category learning we trained  
305 the same models with 20, 40, 60, 80 and 100 images, again for ten “days”, and replayed an equivalent  
306 number of generated representations in each case. To simulate veridical replay, in other words the  
307 replay of each individual experience as it happened, rather than the generation of new samples, we

308 used the activations for each object at that layer in the network during replay periods. These were not  
309 down-sampled during the process. Given how many examples of a concept we generally encounter,  
310 veridical replay of all experience is not a realistic prospect, which is why prior attempts to simulate  
311 replay in smaller-scale networks have also avoided this scenario in their approaches (Kemker and  
312 Kanan 2017; van de Ven et al. 2020). To additionally demonstrate the improvements that replay  
313 affords on each day relative to the previous day, we calculated the performance improvement from  
314 day n to day n+1, divided by the difference between model performance on day n and 1, which  
315 represents the potential room for improvement.

316

### 317 **2.5 Replay within a reinforcement learning framework**

318 We tested a process through which items which are most beneficial for replay might be selected in  
319 the brain. We proposed that such selective replay may involve an interaction between the main  
320 concept learning network (VGG-16), and a smaller network which learned through reinforcement  
321 which concepts are most beneficial to replay through the main network during offline periods. The  
322 neural analogue of such a network could be thought of as the hippocampus, as the activity of this  
323 structure precedes the widespread reactivation of neural patterns observed during replay (Zhang et  
324 al. 2018). This approach is similar to the “teacher-student” meta-learning framework which has been  
325 shown to improve performance in deep neural networks (Fan et al. 2018). The side network was a  
326 simple regression network with 10 inputs, one for each class, and one output, which was the predicted  
327 value for replaying that class through the main network. Classes were chosen and replayed one at a  
328 time, with a batch size of 36. To train the side network, a value of 1 was inputted for the chosen class,  
329 with zeros for the others. The predicted reward for the side network was the change in performance  
330 of the main network after each replay instance, which was quantified by a change in chi-square; a  
331 contrast of the maximum number of possible correct predictions by the main network, versus its  
332 actual correct predictions. A positive reward was therefore a reduction in chi-square, which resulted  
333 in an increase in the side network’s weight for that class. This led to the class being more likely to be

334 chosen in future, as the network's weights were converted into a SoftMax layer, from which classes  
335 were selected probabilistically for replay. Through this iterative process, the side network learned  
336 which classes were more valuable to replay, and continually updated its preferences based on the  
337 performance of the main network. Reducing the chi-square in this dynamic manner improves the  
338 overall network accuracy as it progressively reduces the disparity between the network's  
339 classifications and the actual class identities. To generate initial values for the side network, one batch  
340 of each class was replayed through the main network. The Adam optimiser was used with a learning  
341 rate of 0.001 and the objective was to minimise the mean squared error loss. The side network was  
342 trained for 50 epochs with each replay batch. The assessment of network improvement was always  
343 performed on the validation set, and the reported values are accuracy on the test set, reflecting the  
344 ability of the network to generalise to new situations.

345

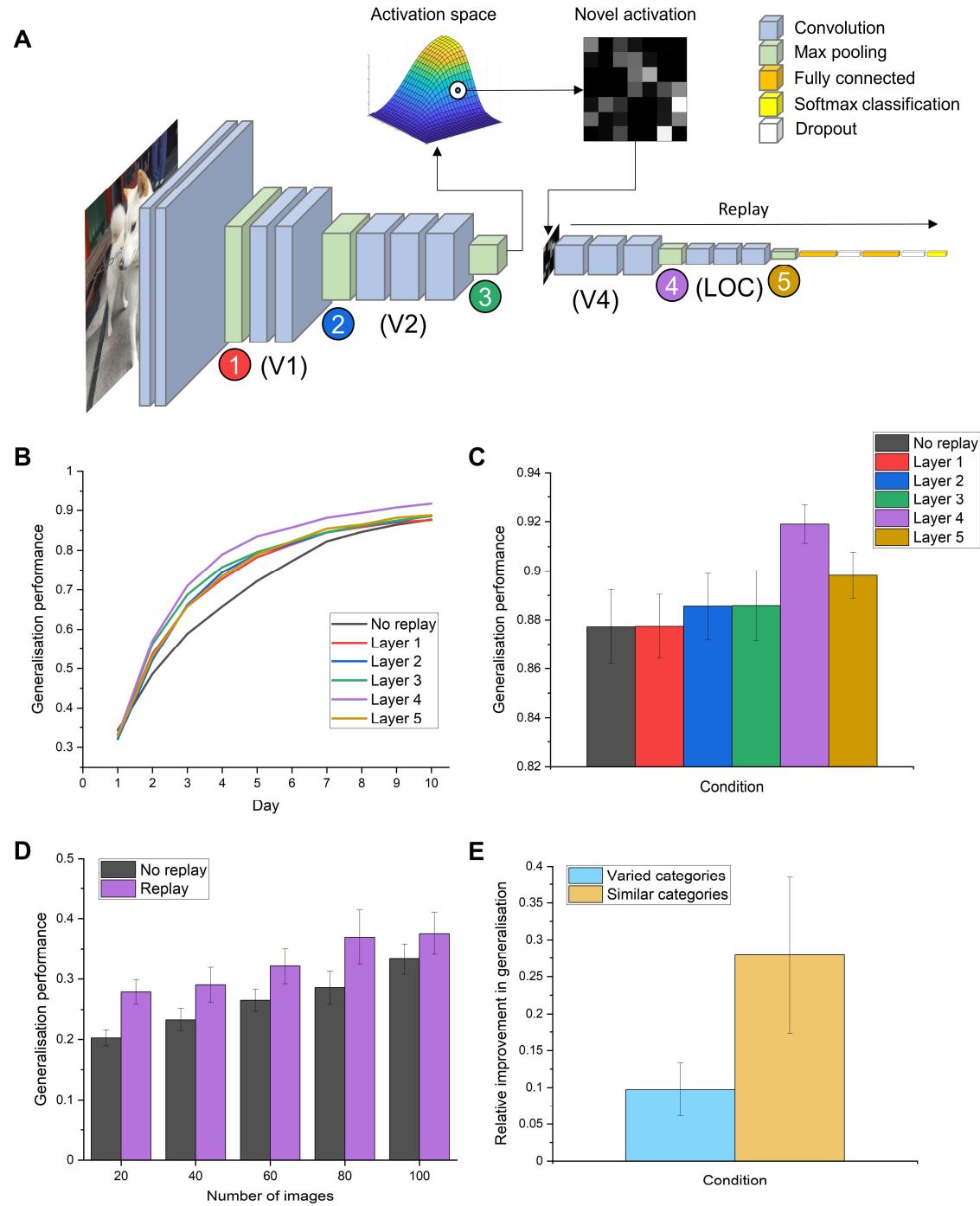
### 346 **3. Results**

#### 347 **3.1 Localising where in the ventral visual stream generative replay is likely to enhance 348 generalisation**

349 We first sought to establish where in the visual brain the replay of category knowledge might be most  
350 effective in helping to generalise to new experiences, as the functional relevance of replay observed  
351 in many different brain regions has yet to be established. To obtain a baseline measure of how the  
352 network would perform without replay, the network learned 10 new categories in the absence of  
353 offline replay. Next, we implemented generative memory replay. To do this, we captured the "typical"  
354 activation of the network for a category and sampled from this gist-like representation to create novel,  
355 abstracted representations for replay (Fig 1A).

356 We simulated generative replay from different layers in the DCNN, equivalent to different  
357 brain regions along the ventral stream. Specifically, we trained the network over 10 epochs, mimicking  
358 10 days of learning in humans, and replayed prototypical representations after each training epoch,

359 simulating 10 nights of offline consolidation during sleep. In Fig 1B we show how replay affects the  
360 ability of the network to generalise to new exemplars of the categories over the course of learning.  
361 Replay substantially speeds up the learning process, with replay from layer four already reaching the  
362 final baseline generalisation performance three days earlier. Fig 1C shows the final best performing  
363 models in each replay condition. A one-way repeated-measures ANOVA on the final models revealed  
364 a difference across conditions ( $F_{(5,45)} = 7.23$ ,  $p < 0.001$ ), with planned Bonferroni-corrected post-hoc  
365 comparisons revealing that only replay from layer 4 ( $t_{(9)} = -4.31$ ,  $p = 0.002$ ) was significantly higher than  
366 baseline. We performed an additional analysis to confirm that the down-sampling of earlier layers did  
367 not explain this finding, by further down-sampling the replay representations in layer four by a factor  
368 of seven, and generalisation performance in this layer was still significantly higher than baseline (see  
369 supplementary Fig 2). Therefore, there is a differential benefit of replay throughout the network,  
370 where replay in the early layers is of limited benefit, whereas replay in the later layers boosts  
371 generalisation performance to a greater degree. This predicts that early visual areas in the brain may  
372 not store sufficiently complex category-specific representations, curtailing the effectiveness of  
373 generated replay representations, whereas areas further along the ventral visual stream, such as the  
374 lateral occipital cortex, might be better positioned to support the generation of novel, prototypical  
375 concepts which accelerates learning in the absence of real experience and helps us to generalise to  
376 new situations. We further investigated if generative replay could benefit category learning where few  
377 exemplars are available. In Figure 2D we show that generative replay from layer four could improve  
378 generalisation when learning and replaying just 20, 40 or 60 exemplars (all t-tests below Bonferroni-  
379 corrected threshold of  $p = 0.01$ ). We also assessed the effects of replay on class disambiguation in this  
380 layer, by training a model containing conceptually highly similar classes collated from all of the other  
381 models, and comparing the relative increase in generalisation performance from the original class  
382 accuracies. Figure 2E shows a replay-induced performance increase for conceptually similar items, but  
383 this did not reach statistical significance ( $t_{(9)} = -2.10$ ,  $p = 0.065$ ).  
384



386 **Fig 1. The effects of generative replay from different layers of a model of the human ventral visual**  
 387 **stream on generalisation to new exemplars. (A)** The VGG-16 network attempts to simulate the brain's  
 388 visual system by looking at photographs and extracting relevant features to help categorise the objects  
 389 within. We trained this network on 10 new categories of objects it had not seen before. In between  
 390 learning episodes, to simulate sleep-facilitated consolidation in humans, we implemented offline

391 memory replay as a generative process. In other words, the network “imagined” new examples of a  
392 category based on the distribution of features it has learned so far for that object (activation space),  
393 and used these representations (novel representation) to consolidate its memory. The network did  
394 not create an actual visual stimulus to learn from, rather it recreated the neuronal pattern of activity  
395 that it would typically generate from viewing an object from that category. We display here an  
396 example of replaying from a mid-point in the network, but all five locations where replay was  
397 implemented are indicated by the coloured circles. The brain regions which have been reported to  
398 contain functionally similar representations to different network layers, derived from Güçlü and van  
399 Gerven (2015), are listed beneath. (B) The effects of memory replay from different layers on the  
400 network’s ability to generalise to new examples of the 10 categories, throughout the course of 10  
401 learning episodes. Plotted values represent the mean accuracies from 10 different models which each  
402 learned 10 new and different categories. (C) The final recognition accuracies (+/- S.E.M.), averaged  
403 across 10 models, on the new set of photographs after 10 epochs of learning. We reveal the location  
404 in a model of the ventral stream where replay maximally enhances generalisation performance is an  
405 advanced layer which bears an approximate functional correspondence to the lateral occipital cortex  
406 (LOC) in humans. The benefits of replay from other locations were less pronounced, with the earliest  
407 layer showing the least benefit to generalisation. (D) The benefits of replay from layer four on  
408 generalisation performance with limited numbers of exemplars (E) The effect of generative replay  
409 from layer four on the generalisation performance of classes when learned alongside diverse  
410 categories or where all are conceptually similar.

411

### 412 **3.2 Tracking the benefits of replay across learning**

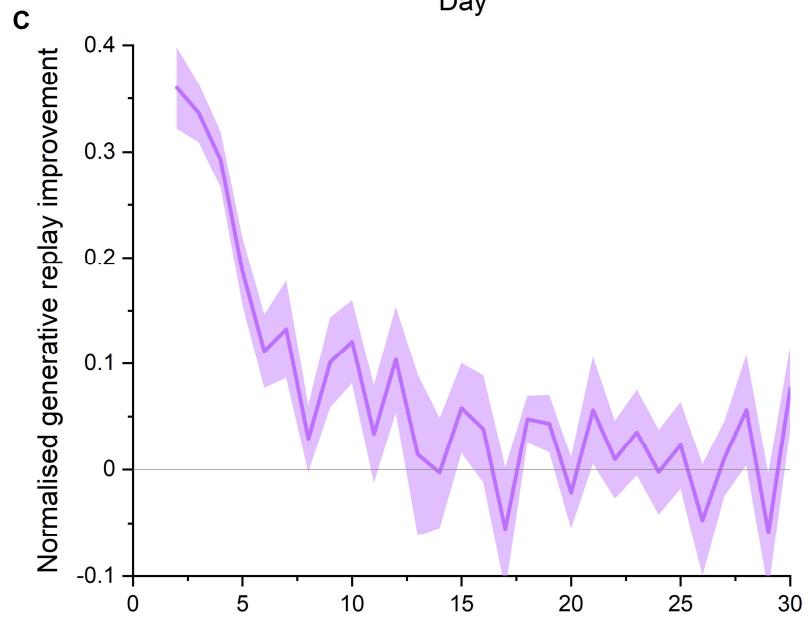
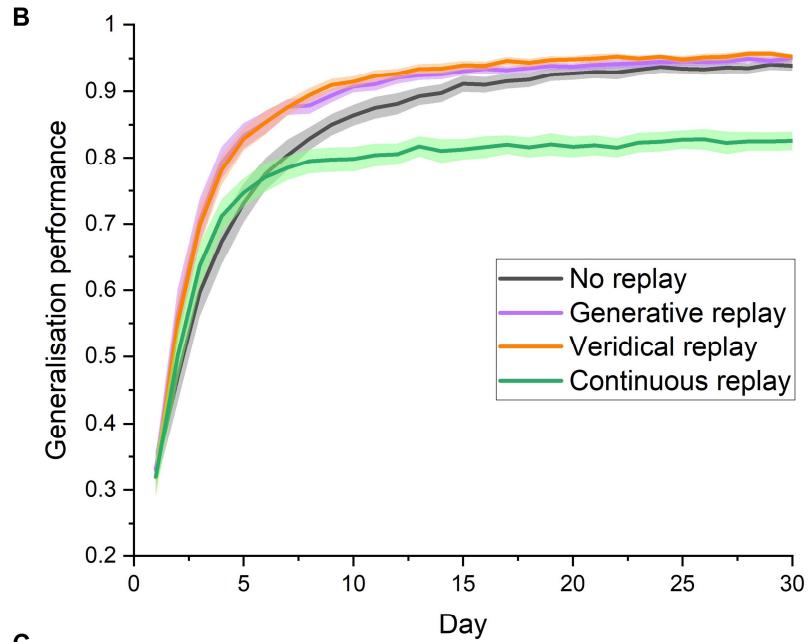
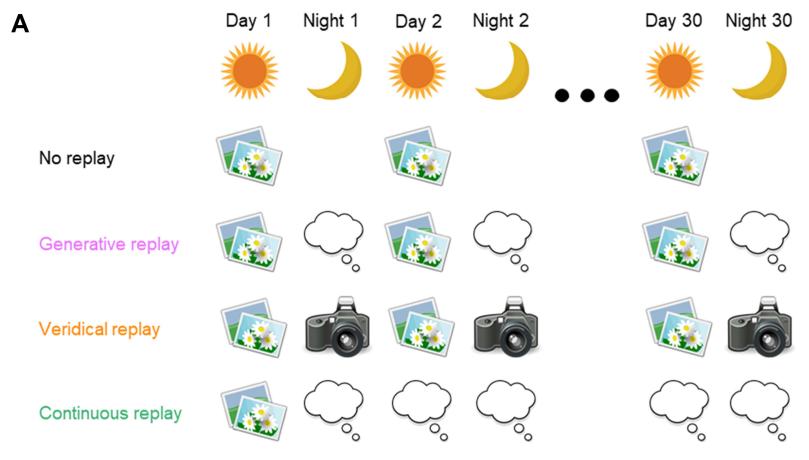
413 In the second experiment, we extended training to 30 days of experience, interleaved with nights of  
414 offline generative replay to simulate learning over longer timescales and predict when in learning  
415 replay might be more effective (Fig 2A). Guided by the results of experiment one, we implemented  
416 replay from an advanced layer corresponding to the lateral occipital cortex. A mixed between-within

417 ANOVA showed an interaction between condition and day ( $F_{(29,522)} = 5.03$ ,  $p < 0.001$ ) with planned  
418 post-hoc Bonferroni-corrected comparisons ( $p < 0.00167$ ) revealing a difference between generative  
419 replay and baseline for days two to six, and eight (Fig 2B). Visualising the network's improvement in  
420 performance from day to day relative to the potential room for improvement from the previous day  
421 confirmed that the benefits of generative replay were limited to early learning (Fig 2C). Therefore,  
422 offline generative replay might be more effective at improving generalisation to new exemplars at the  
423 earliest stages of learning. This suggests replay might facilitates rapid generalisation, which maximises  
424 performance given a limited set of experiences with a category.

425 We were interested to compare generative replay with the unlikely veridical, high-resolution  
426 scenario whereby humans could replay thousands of encounters with individual objects exactly as  
427 they were experienced. We termed this “veridical replay” (Fig 2A), which involved capturing the exact  
428 neural patterns associated with each experienced object during learning, and replaying these from  
429 the same point in the network. A mixed between-within ANOVA did not reveal any difference  
430 between generative and veridical replay in terms of generalisation performance ( $F_{(1,18)} = 0.16$ ,  $p =$   
431  $0.696$ ), nor was an interaction effect observed between day and condition ( $F_{(29,522)} = 0.29$ ,  $p = 0.999$ ,  
432 Fig 2B). Therefore, generative replay was comparably effective to veridical replay of experience in  
433 consolidating memory, despite being entirely imagined from the networks prior experience. This  
434 provides tentative support for the hypothesis that generative replay is a putative form of category  
435 replay in humans, as it would appear vastly more efficient to imagine new concepts from an extracted  
436 prototype.

437 The aforementioned results simulated the benefits of replay under optimal conditions where  
438 humans encounter the same categories every day, however there are instances where exposure will  
439 be limited. To what extent can offline replay compensate for this limited learning? We simulated this  
440 in our model of the ventral stream by limiting the learning of actual category photographs to one day,  
441 and substituted all subsequent learning experiences with offline replay, termed “continuous replay”  
442 (Fig 2A). Despite the absence of further exposure to the actual objects, we found the network could

443 increase its generalisation accuracy from 32% to 83% purely by replaying imagined instances of  
444 concepts it has partially learned. This result may inform our understanding of the human ability to  
445 quickly learn from limited experience. However, a mixed-between ANOVA revealed a statistically  
446 significant interaction effect between day and condition ( $F_{(29,522)} = 3.78$ ,  $p < 0.001$ ), with planned  
447 Bonferroni post-hoc comparisons revealing a difference between generative replay and continuous  
448 replay from day nine onwards (all  $p < 0.00167$ ). Therefore, replayed representations appear to be  
449 dynamic in nature, as the prototypes generated from that first experience were not sufficient to train  
450 the network to its maximum performance, as is observed when learning and replay are interleaved.  
451 This suggests that replayed representations continue to improve as they are informed by ongoing  
452 learning, therefore generative replay in the human brain throughout learning may be envisaged as a  
453 constantly evolving “snapshot” of what has been learned so far about that category.



455 **Fig 2. The facilitatory effects of memory replay across category learning.** We simulate the long-  
456 term consolidation of category memory by extending training to 30 days. (A) Schematic showing the  
457 different experimental conditions. “No replay” involves the model of the visual system learning the  
458 10 new categories without replay in between episodes. “Generative replay” simulates the brain  
459 imagining and replaying novel instances of a category during “night” periods of offline consolidation,  
460 from a layer bearing some functional approximation to the lateral occipital cortex. “Veridical replay”  
461 simulates the hypothetical performance of a human who, each night, replays every single event  
462 which has been experienced the preceding day. “Continuous replay” simulates a single day of  
463 learning, followed by days and nights of replay, investigating the potential benefit afforded by replay  
464 given only brief exposure to a category. For both day-time learning of real images and night-time  
465 consolidation of generated representations, the number of training stimuli was always 1,170 for  
466 each class. (B) The ability of the network to generalise to new exemplars of a category during each  
467 day throughout the learning process. Generalisation performance is measured by the proportion (+/-  
468 S.E.M.) of correctly recognised test images across 10 models. Generative replay maximally increases  
469 performance early in training, suggesting it might be optimal for new learning and recent memory  
470 consolidation. Despite being comprised of internally generated fictive experiences, generative replay  
471 was comparably effective to veridical replay throughout the learning process, positing it as an  
472 attractive, efficient and more realistic solution to memory consolidation which does not involve  
473 remembering all experiences. Continuous replay after just one day of learning substantially  
474 improved generalisation performance, but never reached the accuracy levels of networks which  
475 engaged in further learning. (C) The improvement in performance that generative replay affords on  
476 each day relative to the possible improvements from the previous day.

477

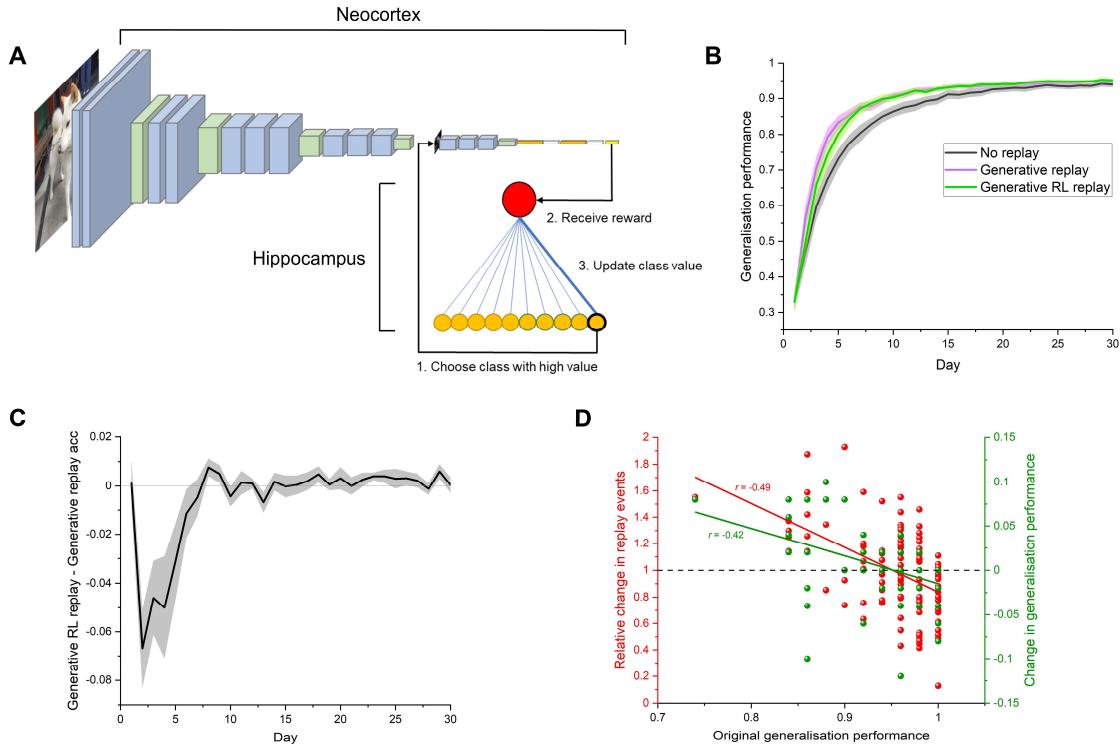
### 478 **3.3 Determining how the brain might select experiences for replay**

479 We proposed that replay may be a learning process in itself, whereby the hippocampus selects replay  
480 items, and learns through feedback from the neocortex the optimal ones to replay. In our previous

481 simulations we selected all categories for replay in equal number, however to simulate the  
482 autonomous nature of replay selection in the brain, we supplemented our model of the ventral visual  
483 stream with a small reinforcement learning network, approximating the theoretical role of the  
484 hippocampus in deciding what to replay (Fig 3A). The hippocampus-like model could choose one of  
485 the 10 categories to replay, and received a reward from the main network for that action, based on  
486 the improvement in network performance.

487 We trained our model of the visual system on 10 novel categories, implementing replay during  
488 offline periods as before, and compared its generalisation performance with that of the dual  
489 interactive hippocampal-cortical model. In terms of overall accuracy, although generative RL replay  
490 appeared to lag briefly behind generative replay at the beginning of training, both approaches  
491 performed similarly, with a mixed between-within ANOVA revealing no difference between the two  
492 conditions in terms of generalisation performance ( $F_{(1,18)} = 0.15$ ,  $p = 0.704$ ), nor was an interaction  
493 effect observed between day and condition ( $F_{(29,522)} = 1.28$ ,  $p = 0.153$ , Fig 3B). Fig 3C plots the  
494 difference between the two conditions across learning. However, the reinforcement learning network  
495 which simulated the hippocampal replay systematically selected categories which were originally  
496 relatively weakly learned more often ( $R^2 = 0.24$ ,  $F_{(1, 98)} = 31.15$ ,  $p < 0.001$ , Fig 3D), which resulted in  
497 their selective improvement ( $R^2 = 0.18$ ,  $F_{(1, 98)} = 21.15$ ,  $p < 0.001$ ). However, this came at a cost, with  
498 originally well-learned categories being replayed less often and a drop in their generalisation accuracy.  
499 We present the idea that such a reinforcement learning process may underlie the “rebalancing” of  
500 experience in the brain, and that replay may therefore help to compensate for the fact that some  
501 categories are more difficult to learn than others.

502



503

504 **Fig 3. Replay as a reinforcement learning process simulates the brain's tendency to consolidate**  
505 **weaker knowledge.** (A) Replay in a model which approximates the visual system is controlled by a  
506 reinforcement learning (RL) network which aims to assume the role of the hippocampus. The RL  
507 network selects one of 10 categories to replay through the visual system and receives a reward  
508 based on the improved performance, learning through trial and error which categories to replay. (B)  
509 Overall generalisation performance on new category exemplars was similar for both generative  
510 replay and generative replay controlled by a reinforcement learning network. Generalisation  
511 performance represents mean accuracy (+/- S.E.M) on test images across 10 models which each  
512 learned 10 new categories. (C) The difference between generative replay and generative RL replay  
513 performance for each day. (D) The RL network learns to replay categories which were originally more  
514 difficult for the model of the visual system, and improves their accuracy. This effectively  
515 “rebalanced” memory such that category knowledge was more evenly distributed, and offers a  
516 candidate mechanism as to how the brain chooses weakly learned information for replay. Plotted

517 values represent the 100 categories across 10 models. A proportion of the generalisation  
518 performance values are overlapping.

519

## 520 **4. Discussion**

521 We simulated the consolidation of category knowledge in a large-scale neural network model which  
522 approximates functional aspects of the human ventral visual system, by replaying prototypical  
523 representations thought to be formed and initiated by the hippocampus. The notion that replay of  
524 visual experiences might be generative in nature has been suggested by limited-capacity models which  
525 have been trained on low-resolution photographic images (van de Ven et al. 2020). However, our  
526 results using a model of the visual brain whose representations has compared favourably with actual  
527 brain data, represent more persuasive evidence that humans are unlikely to replay experiences  
528 verbatim during rest and sleep to improve category knowledge, and might be more likely to replay  
529 novel, imagined instances instead. In addition, the large number (117,000) of high-resolution complex  
530 naturalistic images we used for training in this experiment more closely reflected real-world learning  
531 and facilitated the extraction of gist-like features. While empirical evidence exists that humans replay  
532 novel sequences of stimuli (Liu et al. 2019), our work suggests that the brain might go further and uses  
533 learned features of objects to construct entirely fictive experiences to replay. We speculate that this  
534 creative process is particularly important for the consolidation of category knowledge as opposed to  
535 the replay of episodic memory (Deuker et al. 2013; Schapiro et al. 2018; Zhang et al. 2018), because  
536 of the requirement to abstract prototypical features and use these to generalise to new examples of  
537 a category. We propose that generative replay confers additional advantages such as constituting less  
538 of a burden on memory resources, as not all experiences need to be remembered. Further, our replay  
539 representations were highly effective in consolidating category knowledge despite being down-  
540 sampled, and these compressed, low-resolution samples would reduce storage requirements further.  
541 Perhaps the simulation that most favourably supported the hypothesis that category replay in the  
542 brain likely adopts this compressed, prototypical format is that it aided generalisation to a similar

543 degree as the exact veridical replay of experience in boosting generalisation performance. Therefore,  
544 the main advantage to generative replay over veridical replay is that it represents a feasible, efficient  
545 solution to memory consolidation without compromising effectiveness. In addition, generative replay  
546 can add to events which have been experienced. Our findings therefore encourage a  
547 reconceptualization of the nature of consolidation-related replay in humans, that it is not only  
548 generative, but also low resolution or “blurry”, as is the case with internally generated imagery in  
549 humans (Giusberti et al. 1992; Lee et al. 2012). In fact, the kind of replay we propose here may be the  
550 driving force behind the transformation of memory into a more schematic, generalised form which  
551 preserves regularities across experiences while allowing unique elements of experience to fade (Love  
552 and Medin 1998; Winocur and Moscovitch 2011; Sweegers and Talamini 2014). The challenge for  
553 future empirical studies in humans to confirm our hypothesis, will be to decode prototypical replay  
554 representations during rest and sleep. In addition, future modelling and empirical work should address  
555 the sequential nature of learning and replay, as life experience does not consist of still snapshots of  
556 experience, such as those used in these experiments. Prior modelling work has shown that a video  
557 game-playing agent can improve its performance by learning inside its own generated environment  
558 (Ha and Schmidhuber 2018), which is more akin to an unfolding dream during sleep, and may provide  
559 inspiration for modelling the generative replay of video-like events to support category learning.

560 Simulating replay in a human-like network also allowed us to answer a question not currently  
561 tractable in neuroimaging studies: where in the visual stream is replay functionally relevant to  
562 consolidation? In a prior simulation of replay in a neural network, van de Ven et al. (2020)  
563 demonstrated generative replay could attenuate forgetting when performed after the final  
564 convolutional layer, but its effectiveness was not compared to earlier layers, and the network  
565 employed, consisting of five convolutional layers, had not been compared with the human visual  
566 system. Deeper networks, such as the one used here, consisting of 23 layers in total, organised into  
567 five blocks of convolutional layers, not only extract useful category features from naturalistic images,  
568 but representations in network layers have demonstrated a degree of representational

569 correspondence with specific brain regions along the ventral visual stream (Khaligh-Razavi and  
570 Kriegeskorte 2014; Güçlü and van Gerven 2015; Devereux et al. 2018), albeit not capturing all  
571 observable variance (Xu and Vaziri-Pashkam 2021). In keeping with our observation that low-  
572 resolution, coarse, schematic replay was effective in helping the network to generalise, we found the  
573 most effective location for replay to be in the most advanced layers of the network, layers which are  
574 less granular in their representations. This region shares some functional similarities with the lateral  
575 occipital cortex in humans, a region which represents more complex, high-level features (Güçlü and  
576 van Gerven 2015). In contrast, generative replay from the earliest layers corresponding to early visual  
577 cortex was less effective. These layers are sensitive to low-level visual features such as contrast, edges  
578 and colour, therefore generating samples from these layers will yield rudimentary-level category-  
579 specific information, which are of limited utility for replay and generalisation. High-level  
580 representations on the other hand, may contain more unique combinations and abstractions of these  
581 lower-level features. We also found replay from the penultimate layer was more effective than the  
582 final layer, suggesting the optimal replay location represents a balance between the presence of  
583 sufficiently complex category information and the number of downstream neuronal weights available  
584 to be updated based on replaying these features. These findings may encourage a re-evaluation of the  
585 functional relevance of replay in early visual cortices in both animals and humans, and generate  
586 specific hypotheses for potential perturbation studies to investigate the effects of disruptive  
587 stimulation at different stages of the ventral stream during offline consolidation.

588 Our simulations also revealed a phenomenon never before tested in humans, that the  
589 effectiveness of replay depends on the stage of learning. We acquire factual information about the  
590 world sporadically over time across contexts, for example we may encounter a new species at a zoo  
591 one day, and subsequently see the same animal on a wildlife documentary, and so on. Ultimately the  
592 consolidation of semantic information in the neocortex can take up to years to complete (Manns et  
593 al. 2003). However, our simulations suggest that replay may be most beneficial during the initial  
594 encounters with a novel category, when we are still working out its identifiable features and have not

595 yet learned to generalise perfectly to unseen instances. It is therefore possible humans replay a  
596 category less and less with increasing familiarity, and there is some support for this idea in the animal  
597 literature (Giri et al. 2019). We speculate that if this is the case, the enhanced effectiveness for recent  
598 memories may have an adaptive function, allowing us to generalise quickly with limited information.  
599 In fact, our simulations showed that after a single learning episode, replay can compensate  
600 substantially for an absence of subsequent experience. Our results provide novel hypotheses for  
601 human experiments, testing for an interaction between the stage of category learning and the extent  
602 of replay. The fact that replay early in the learning process was more effective provides further support  
603 for our proposal that vague, imprecise replay events are useful for generalisation, as the networks  
604 imaginary representations at that stage would be an imperfect approximation of the category in  
605 question. We acknowledge there may be a “ceiling effect”, whereby later in training there is no further  
606 room for improvement, however we would posit that over the human lifespan, we are operating in  
607 the non-converged portion of the learning curve that we display here.

608 Our results also represent the first mechanistic account of how the brain selects weakly-  
609 learned information for replay and consolidation (Kuriyama et al. 2004; Drosopoulos et al. 2007;  
610 McDevitt et al. 2015; Schapiro et al. 2018). The hippocampus triggers replay events in the neocortex  
611 (Zhang et al. 2018), with a loop of information back and forth between the two brain areas (Rothschild  
612 et al. 2017), although the content of this neural dialogue is not known. Our simulations suggest that  
613 the hippocampus may learn the optimal categories to replay based on feedback from the neocortex.  
614 Our results showed that such a process resulted in the “rebalancing” of experience in an artificial  
615 neural network, where generalisation performance was improved for weakly learned items, and  
616 attenuated for items which were strongly learned. A reorganisation of knowledge of this kind has been  
617 observed in electrophysiological investigations in rodents, where the neural representations of novel  
618 environments are strengthened through reactivation at the peak of the theta cycle, while those  
619 corresponding to familiar environments are weakened through replay during the trough (Poe et al.  
620 2000). This more even distribution of knowledge could be adaptive in both ensuring adequate

621 recognition performance across all categories and forming a more general foundation on top of which  
622 future conceptual knowledge can be built. There have been recent theoretical and empirical  
623 demonstrations of how items get selected for replay within a reinforcement learning framework, such  
624 as the “tagging” of items that elicit a large prediction error during the learning phase (Momennejad  
625 et al. 2018), and the replay of events that are more likely to be encountered in future and which lead  
626 to the highest reward (Mattar and Daw 2018; Liu et al. 2021). However, these accounts do not explain  
627 why even in the absence of such prediction errors, or without knowing the likelihood of future events,  
628 knowledge which has been weakly-learned during waking periods is consistently targeted for replay  
629 and consolidation during sleep (Kuriyama et al. 2004; Drosopoulos et al. 2007; McDevitt et al. 2015;  
630 Schapiro et al. 2018). Our interactive networks suggest that offline reinforcement learning could  
631 account for the selection of weakly-learned knowledge during the replay process itself, and future  
632 experiments could assess whether our models choose the same categories for replay as humans when  
633 trained on the same stimuli.

634 In summary, our simulations provide supportive evidence that category replay in humans is a  
635 generative process and make the prediction that it is functionally relevant at advanced stages of the  
636 ventral stream. We have generated hypotheses about when during learning replay is likely to be  
637 effective and offer a novel account of replay as a learning process in and of itself between the  
638 hippocampus and neocortex. We hope these findings encourage a closer dialogue between theoretical  
639 models and empirical experiments. These findings also add credence to the emerging perspective that  
640 deep learning networks are powerful tools which are becoming increasingly well-positioned to resolve  
641 challenging neuroscientific questions (Richards et al. 2019).

642

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649

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651 investigation, formal analysis, visualization, writing-original draft preparation, writing-review &  
652 editing. B.C.L.: Conceptualization, methodology, resources, funding acquisition, supervision, writing-  
653 review & editing.

654

655 **Data and Code Availability:** The code, environment, and additional information required to run the  
656 simulations is available at <https://github.com/danielbarry1/replay.git> and in the supplementary  
657 information. All relevant data in the paper is available at  
658 <https://doi.org/10.6084/m9.figshare.14208470>.

659

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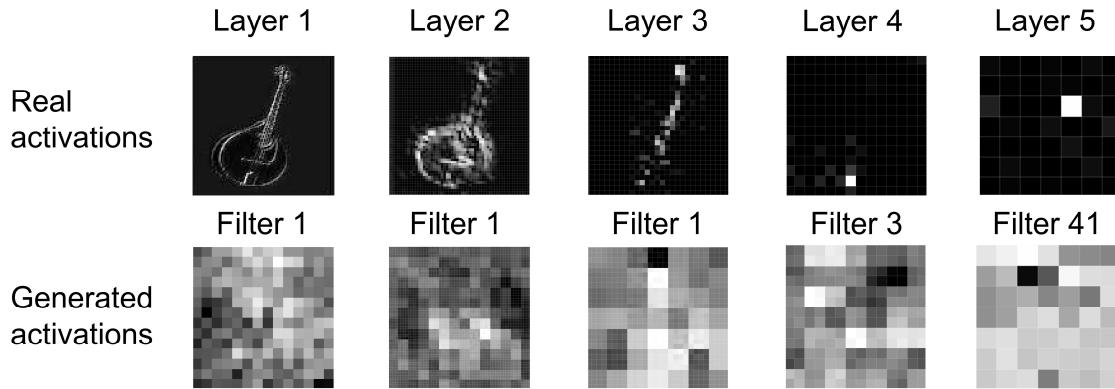
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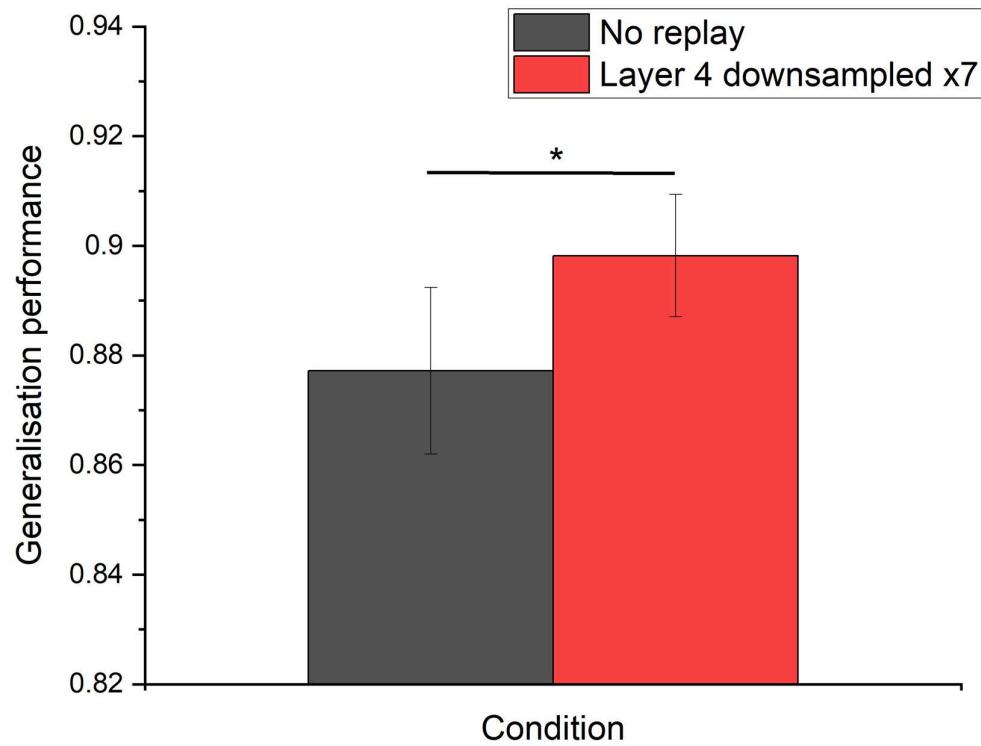
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Supplementary Fig 1. Samples of real and generated activations from different layers in the network, displayed as greyscale images. The first filters where information was visible is displayed.

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Supplementary Fig 2. Generalisation performance improvement over baseline for replay from layer four when downsampled by a factor of seven.

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827 Supplementary table 1: List of ImageNet classes by model

Model 1	n12360108 begonia n02822579 bedstead bedframe n02427724 waterbuck n03098688 control room n02944075 camisole n01603600 waxwing n03196598 digital display alphanumeric display n02848216 blade n07712856 tortilla chip n03592669 jalouse
Model 2	n11853356 Christmas cactus Schlumbergera buckleyi Schlumbergera baridgesii n04177820 settle settee n03904183 pedestrian crossing zebra crossing n04355511 sundress n03487444 hand lotion n12899752 angel's trumpet Brugmansia suaveolens Datura suaveolens n12655869 raspberry raspberry bush n12948053 common European dogwood red dogwood blood-twig pedwood Cornus sanguinea n02869737 bongo bongo drum n02415253 Dall sheep Dall's sheep white sheep Ovis montana dalli
Model 3	n03375575 foil n03082807 compressor n03262932 easy chair lounge chair overstuffed chair n02047614 puffin n03317788 faience n09475044 wasp's nest wasps' nest hornet's nest hornets' nest n11784497 jack-in-the-pulpit Indian turnip wake-robin Arisaema triphyllum Arisaema atrorubens n03941231 pinata n02813399 bay window bow window n04544325 wainscoting wainscotting
Model 4	n03993053 potty seat potty chair n04082886 reticule reticule graticule n03421324 garter belt suspender belt n03766044 miller milling machine n03505504 headscarf n12384839 love-in-a-mist running pop wild water lemon Passiflora foetida n03619793 kitbag kit bag n07600696 candied apple candy apple taffy apple caramel apple toffee apple n02068974 dolphin n03237992 dressing gown robe-de-chambre lounging robe
Model 5	n02918964 bumper car Dodgem n02392824 white rhinoceros Ceratotherium simum Diceros simus

	n01806364 blue peafowl <i>Pavo cristatus</i>
	n02956699 capitol
	n04290079 spun yarn
	n08596076 littoral litoral littoral zone sands
	n02887970 bracelet bangle
	n10635788 sphinx
	n07901457 muscat muscatel muscadel muscadelle
	n07870167 lasagna lasagne
Model 6	n04324387 stockroom stock room
	n04591517 wind turbine
	n02988486 CD-R compact disc recordable CD-WO compact disc write-once
	n04568069 weathervane weather vane vane wind vane
	n04514241 uplift
	n03207835 dishtowel dish towel tea towel
	n13206817 maidenhair maidenhair fern
	n03307792 external drive
	n12666965 cape jasmine cape jessamine <i>Gardenia jasminoides</i> <i>Gardenia augusta</i>
	n12950126 valerian
Model 7	n03986355 portfolio
	n11848479 night-blooming cereus
	n04439712 tinfoil tin foil
	n03160740 damask
	n01612122 sparrow hawk American kestrel kestrel <i>Falco sparverius</i>
	n09206896 arroyo
	n12392549 stinging nettle <i>Urtica dioica</i>
	n02343772 gerbil gerbille
	n07875436 risotto Italian rice
	n02060133 fulmar fulmar petrel <i>Fulmarus glacialis</i>
Model 8	n03655072 legging leging leg covering
	n10738111 unicyclist
	n09270735 dune sand dune
	n03409393 gable gable end gable wall
	n02331046 rat
	n03452267 gramophone acoustic gramophone
	n10105733 forward
	n07911677 cocktail
	n03797182 muffler
	n01563128 warbler
Model 9	n04197110 shipwreck
	n10470779 priest
	n02769290 backhoe
	n03478756 hall
	n04519153 valve
	n04289027 sprinkler
	n02782778 ballpark park

	n03558404 ice skate
	n04138261 satin
	n02700064 alternator
Model 10	n03524150 hockey stick
	n03716966 mandolin
	n02962200 carburetor carburettor
	n03237340 dresser
	n04004210 printed circuit
	n02917377 bullhorn loud hailer loud-hailer
	n07879953 tempura
	n04087826 ribbing
	n02404432 longhorn Texas longhorn
	n07830593 hot sauce

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847 Supplementary table 2: Conceptually similar classes (plants)

Model 1 (1)	n12360108 begonia
Model 2 (1)	n11853356 Christmas cactus Schlumbergera buckleyi Schlumbergera baridgesii
Model 2 (6)	n12899752 angel's trumpet Brugmansia suaveolens Datura suaveolens
Model 2 (8)	n12948053 common European dogwood red dogwood blood-twigs pedwood Cornus sanguinea
Model 4 (6)	n12384839 love-in-a-mist running pop wild water lemon Passiflora foetida
Model 6 (7)	n13206817 maidenhair maidenhair fern
Model 6 (9)	n12666965 cape jasmine cape jessamine Gardenia jasminoides Gardenia augusta
Model 6 (10)	n12950126 valerian
Model 7 (2)	n11848479 night-blooming cereus
Model 7 (7)	n12392549 stinging nettle Urtica dioica

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