
Brain-like Flexible Visual Inference by Harnessing Feedback-Feedforward Alignment

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Abstract

1 In natural vision, feedback connections support versatile visual inference capabilities
2 such as making sense of the occluded or noisy bottom-up sensory information
3 or mediating pure top-down processes such as imagination. However, the mechanisms
4 by which the feedback pathway learns to give rise to these capabilities flexibly
5 are not clear. We propose that top-down effects emerge through alignment
6 between feedforward and feedback pathways, each optimizing its own objectives.
7 To achieve this co-optimization, we introduce Feedback-Feedforward Alignment
8 (FFA), a learning algorithm that leverages feedback and feedforward pathways
9 as mutual credit assignment computational graphs, enabling alignment. In our
10 study, we demonstrate the effectiveness of FFA in co-optimizing classification and
11 reconstruction tasks on widely used MNIST and CIFAR10 datasets. Notably, the
12 alignment mechanism in FFA endows feedback connections with emergent visual
13 inference functions, including denoising, resolving occlusions, hallucination, and
14 imagination. Moreover, FFA offers bio-plausibility compared to traditional back-
15 propagation (BP) methods in implementation. By repurposing the computational
16 graph of credit assignment into a goal-driven feedback pathway, FFA alleviates
17 weight transport problems encountered in BP, enhancing the bio-plausibility of the
18 learning algorithm. Our study presents FFA as a promising proof-of-concept for
19 the mechanisms underlying how feedback connections in the visual cortex support
20 flexible visual functions. This work also contributes to the broader field of visual
21 inference underlying perceptual phenomena and has implications for developing
22 more biologically inspired learning algorithms.

23 1 Introduction

24 Humans possess remarkable abilities to infer the properties of objects even in the presence of
25 occlusion or noise. They can mentally imagine objects and reconstruct their complete forms, even
26 when only partial information is available, regardless of whether they have ever seen the complete
27 form before. The process of visual inference on noisy or uncertain stimuli requires additional time,
28 implying cognitive processes that go beyond a simple feedforward pass on visual input and suggest the
29 involvement of additional mechanisms such as feedback and recurrence (Kar et al., 2019; Kietzmann
30 et al., 2019; Gilbert and Sigman, 2007; Debes and Dragoi, 2023; Kreiman and Serre, 2020). Despite
31 the abundant evidence on the involvement of feedback connections in various cognitive processes,
32 understanding the precise mechanisms through which they flexibly give rise to the ability to infer or
33 generate perceptual experiences is not clear.

34 While hierarchical feedforward models of the ventral visual cortex based on deep learning of dis-
35 criminative losses have achieved remarkable success in computer vision tasks (Yamins et al., 2014;
36 Khaligh-Razavi and Kriegeskorte, 2014; Lindsay, 2021), alternative frameworks, such as predictive

37 processing models, offer a distinct perspective on visual processing. Predictive processing models
38 propose that the brain generates fine-grained predictions about incoming sensory inputs and compares
39 them with actual sensory signals to minimize prediction errors (Rao and Ballard, 1999; Friston, 2009;
40 Clark, 2013). These models emphasize the role of feedback connections in the visual cortex, with
41 higher-level areas sending top-down predictions to lower-level areas to guide perception. Unlike
42 deep learning models that learn from large-scale datasets, predictive processing models prioritize
43 the role of prior knowledge and expectations in shaping perception as originally emphasized as far
44 back as Helmholtz (Helmholtz et al., 1909). By incorporating generative models, these frameworks
45 provide a mechanism for understanding how the brain actively constructs visual representations and
46 resolves ambiguities, including the perception of occluded or uncertain stimuli. While predictive
47 processing models emphasize the active role of top-down predictions and prior knowledge in shaping
48 visual perception, they lag behind feedforward models in mechanistic specificity and thus direct
49 neurophysiological evidence (Walsh et al., 2020; Clark, 2013; Keller and Mrsic-Flogel, 2018).

50 Another main constraint on the space of models is the learning algorithm to train the model. Classical
51 error backpropagation (BP) has been a workhorse algorithm for training discriminative, feedforward
52 deep neural networks, particularly for visual object recognition (Rumelhart et al., 1986; Krizhevsky
53 et al., 2012). Despite its immense success in training the state-of-the-art, BP has been critiqued on a
54 number of implementational issues, some of which also call into question its bio-plausibility for the
55 brain: weight symmetry requires weight transport to the feedback network (Grossberg, 1987), the
56 feedback network is not used during runtime inference, and feedforward discrimination performance
57 is not robust to noise (Goodfellow et al., 2015; Akrouf, 2019). Beyond these issues, BP is an infinites-
58 imally local estimate of the gradient, and other higher-order methods for computing the gradient
59 could accelerate learning. As pointed out by Bengio (2014), the inverse of the weight matrix, rather
60 than the transpose, may provide a valid path for credit assignment, learning a linear extrapolation of
61 the underlying landscape (Bengio, 2014). However, attempts to match BP by learning the inverse
62 weights instead of the transpose in a stage-wise fashion, also called target propagation (TP), have
63 yielded limited practical success for reasons that are not entirely clear (Lee et al., 2014; Bartunov
64 et al., 2018)– potentially related to the difficulty of learning an inverse function using noisy gradients
65 as opposed to the relative ease of taking a transpose, a noiseless procedure (Kunin et al., 2020).

66 Here, we simultaneously learn feedforward and feedback functions that are mutual global inverses of
67 each other such that each path can perform credit assignment for the other during the training pass.
68 We term this Feedback-Feedforward Alignment (FFA) since the discriminator (encoder) contributes
69 the gradients for the reconstructor (decoder) and vice versa. We show that rather than trading against
70 each other as in typical, single-objective settings, co-optimizing discrimination and reconstruction
71 objectives can lead to a mutualistic symbiotic interaction.

72 Next, we explore the potential of the gradient path as a model of feedback connections. Inspired by
73 the structural similarity of the credit assignment computational graph and the feedforward pass which
74 parallels the anatomically reciprocated forward and feedback connections in the visual cortex (Markov
75 et al., 2013, 2014). Importantly we hypothesized an objective function for feedback connections
76 motivated by the *High-resolution buffer hypothesis* by Lee and Mumford (2003) regarding the
77 primary visual cortex (V1), arguing that V1 is uniquely situated to act as a high-resolution buffer to
78 synthesize images through generative processes. We hypothesized that by co-tuning feedforward and
79 feedback connections to optimize two different but dependent objective functions, we could explain
80 the properties of flexible visual inference of visual detail under occlusion, denoising, dreaming, and
81 mental imagery.

82 The contributions of this study are as follows:

- 83 • Based on the role of feedback connections in the brain, we propose a novel strategy to train
84 neural networks to co-optimize for two objective functions.
- 85 • We leverage the credit assignment computational graph as feedback connections during
86 learning and inference.
- 87 • We suggest and verify that training feedforward and feedback connections for discrimination
88 and reconstruction respectively, induces noise robustness.
- 89 • We show that FFA can flexibly support an array of versatile visual inferences such as
90 resolving occlusion, hallucination, and visual imagery.

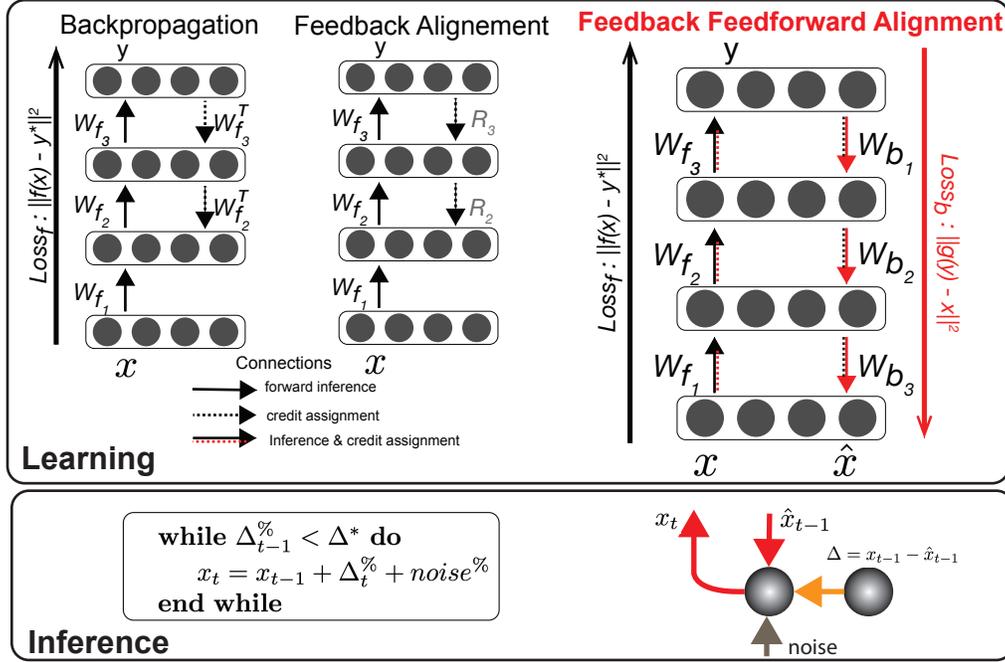


Figure 1: Feedback Feedforward Alignment. Learning: backpropagation and feedback alignment train a discriminator with symmetric W_f^T or fixed random R_i weights, respectively. FFA maps input x to latents y as in a discriminator but also reconstructs the input \hat{x} from the latent. The forward and backward pathways also pass gradients back for their counterpart performing inference in the opposite direction. Inference: We run forward and feedback connections trained under FFA in a loop to update the activations (x) for each of the inference tasks e.g. mental imagery. Δ shows the difference between the input signal and the reconstructed (output). % denotes adjusted value to accommodate convergence. * shows the desired value. See algorithm 1 in Section 8.4

91 2 Related Work

92 2.1 Models of visual perception and inference in the brain

93 In going beyond purely feedforward models, there is a large hypothesis space of recurrent neural
 94 network models (RNNs), and training inference into an RNN via backpropagation through time raises
 95 severe questions about bio-plausibility of the learning algorithm as well as architecture (Lillicrap and
 96 Santoro, 2019). Prior work on RNNs for visual classification whether through complex architecture
 97 search (Nayebi et al., 2022) or through imposing theoretically motivated lateral recurrent connections
 98 (Tang et al., 2014, 2018) has shown benefits for the classification loss but was not geared to improve
 99 our understanding of how feedback or recurrence supports inference of visual details. On the other
 100 hand, there is increasing evidence supporting distinct phases of processing pertaining to perception and
 101 inference which parallels the notion of bottom-up versus top-down processing. Recent studies suggest
 102 that feedforward and feedback signaling operate through distinct "channels," enabling feedback
 103 signals to influence the forward processing without directly affecting the forward-propagated activity
 104 (Semedo et al., 2022; Kreiman and Serre, 2020). Thus, implementing recursion through feedforward
 105 and feedback-dominated phases, as we suggest in FFA, has an anatomical and physiological basis.

106 Internally generated perceptual experiences, such as hallucinations, dreams, and mental imagery evoke
 107 vivid experiences that mimic the perception of real-world stimuli. Neuroimaging studies demonstrate
 108 an overlap in neural activation between internally generated experiences and perception suggesting a
 109 shared neural substrate for generating and processing sensory information (Ganis et al., 2004; Pearson,
 110 2019; Pearson et al., 2008; Abid et al., 2016; Dijkstra et al., 2017). While studies have provided
 111 insights into the brain regions involved in these phenomena, the neural mechanisms and computations
 112 underlying hallucination and imagery remain a topic of ongoing research and debate. One challenge is

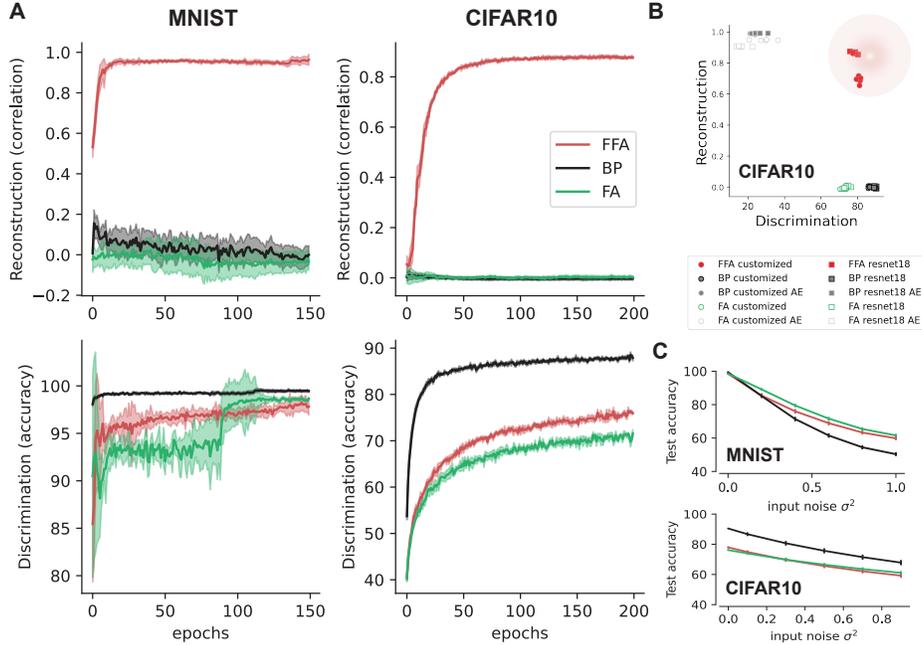


Figure 2: Co-optimization in FFA. A) Accuracy and reconstruction performance for FFA and control algorithms as a function of epochs. B) Dual-task performance for a variety of feedforward discriminative and autoencoder architectures trained under BP or FA compared to FFA training. The shaded area represents the desired corner. C) Robustness to input Gaussian noise as measured by test accuracy on the noisy input.

113 that hallucinations and imagery are subjective experiences that are difficult to objectively measure and
 114 study (Pearson et al., 2008). Additionally, the neural correlates of these experiences can vary across
 115 individuals and different types of hallucinations (Suzuki et al., 2017, 2023). Thus, computational
 116 modeling of how comparable phenomena can emerge in neural networks, without explicitly training
 117 for complex non-bio-plausible generative objective functions, helps elucidate the neural mechanisms
 118 that may underpin these internally-generated perceptions.

119 2.2 Bio-plausible training

120 Our work also falls within the class of bio-plausible extensions of the original BP algorithm that try to
 121 avoid the weight transport problem (Grossberg, 1987). One line of work uses a strategy that still aims
 122 for BP-like symmetric weights while circumventing weight transport by designing a training objective
 123 for the feedback path that encourages symmetry (Akrouf et al., 2019). For example, augmenting a
 124 reconstruction loss with weight decay will constrain solutions to the transpose in the linear setting
 125 (Kunin et al., 2019, 2020). However, our method differs in two key ways. First, those methods require
 126 invoking a separate gradient pass to train the feedback weights whereas we accomplish the training
 127 of feedback with the same feedforward network, thus adding no other hidden paths. Second, those
 128 methods explicitly seek symmetry whereas we do not constrain the stage-wise feedback weights, only
 129 their end-to-end goal. Our algorithm resembles the stage-wise reconstruction in target propagation
 130 (TP) which could also result in end-to-end propagation of latent representations back to inputs if
 131 noise at each local propagation step is sufficiently small (Bengio, 2014; Lee et al., 2014). Unlike
 132 the original TP, we do not constrain the intermediate stages and do not use any BP training on the
 133 penultimate layer of the discriminator.

134 3 Feedforward and feedback alignment

135 During the training, BP uses a computational graph to backpropagate the error to the hidden layers
 136 Figure 1. This computational graph is a linear neural network that is the transpose of the forward

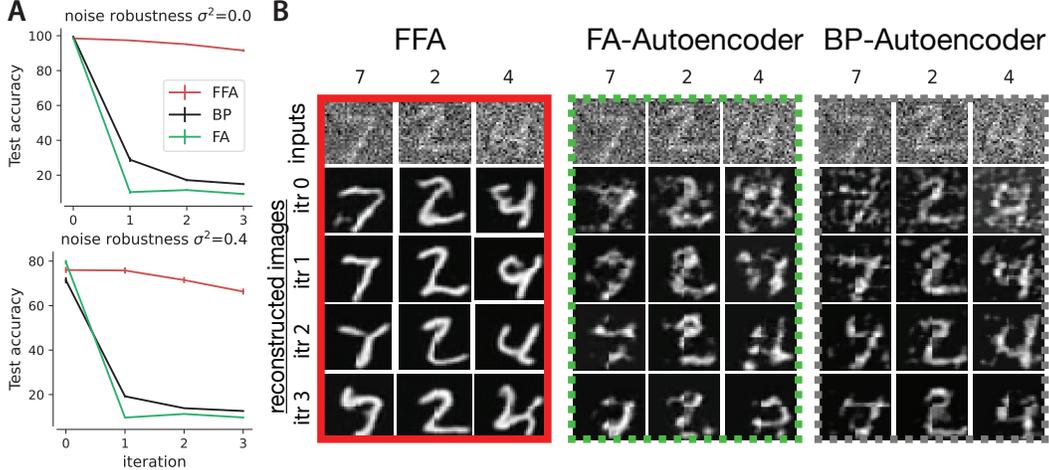


Figure 3: Denoising in FFA. Closed-loop inference on noisy inputs ($\sigma^2 = 0.4$) performed by FFA and control algorithms assuming a static read-out for discrimination set by iteration 0. Shown at right, the sample reconstructions recovered by FFA and control autoencoders over 4 iterations (no clipping or other processing was performed on these images).

137 neural network and is constantly updated every time the forward weights are updated. FA and in
 138 general the family of the random feedback gradient path such as DFA, use random values and do
 139 not update the backward weights during the training. FFA in essence runs two FA algorithms to
 140 train the forward pass and backward pass alternatively. The FFA diagram in Figure 1 highlights
 141 its two distinguishing features: feedback (decoder) has an end-to-end goal and co-opting of the
 142 forward discriminator path (encoder) to train this decoder. Below, we compare how FFA operates on
 143 MNIST across two architectures (fully connected and convolutional) and on CIFAR10 using a ResNet
 144 architecture by directly reconstructing from the ten-dimensional discriminator output. For details on
 145 the architecture please refer to Supplementary material 8.1. For each architecture, we compare FFA
 146 to BP and feedback alignment (FA) (Lillicrap et al., 2016) training of a single objective (feedforward
 147 discrimination or an autoencoder loss) resulting in 5 control models: FFA, BP, FA, BP-AE, and
 148 FA-AE. The purpose of these controls was to verify that the properties of gradient descent on a single
 149 loss does not trivially invoke reconstruction of input for example in BP-trained networks.

150 3.1 FFA achieves the co-optimization of discrimination and reconstruction

151 We highlight performance results on a convolutional architecture but also report results on a fully
 152 connected architecture. Convolutional architectures are potentially of greater interest because they
 153 are used for scaling up algorithms to larger datasets. Furthermore, convolutional architectures tend to
 154 expose greater performance gaps between BP and FA (Bartunov et al., 2018). FFA-trained networks
 155 achieved digit discrimination performance on par with FA but slightly below BP (Figure 2). However,
 156 on MNIST, discrimination performance is exceedingly high. Critically, we were also interested in
 157 seeing if FFA could co-train, using only the discriminator weights for credit assignment, a digit
 158 reconstruction path. We found that FFA produced reconstruction on par with a BP-trained autoencoder
 159 for convolutional architectures while slightly lagging the autoencoder standard for reconstruction
 160 on fully connected architectures. Thus, within the same network, FFA co-optimizes two objectives
 161 at levels approaching the high individual standards set by a BP-trained discriminator and a BP-
 162 trained reconstructor (see Figure 2 and Supp. Figure 7). In FFA, like FA, the feedforward and
 163 feedback weights aligned over training (Lillicrap et al., 2016), but only in FFA, alignment is useful
 164 for reconstruction, presumably because both paths are free to align to each other which breaks the
 165 random feedback constraint of FA. In examining discrimination versus reconstruction performance,
 166 these can be mutually exclusive. For example, single objective networks tend to improve along
 167 one axis or the other. In contrast, FFA-trained networks moved toward the top-right corner of the
 168 plot indicating co-optimization along both axes (Figure 2, scatter plot). As shown in Figure 2 B
 169 for CIFAR10, FFA and FA both struggle to keep up with BP, so for the rest of the paper regarding
 170 inference, we focus on MNIST.

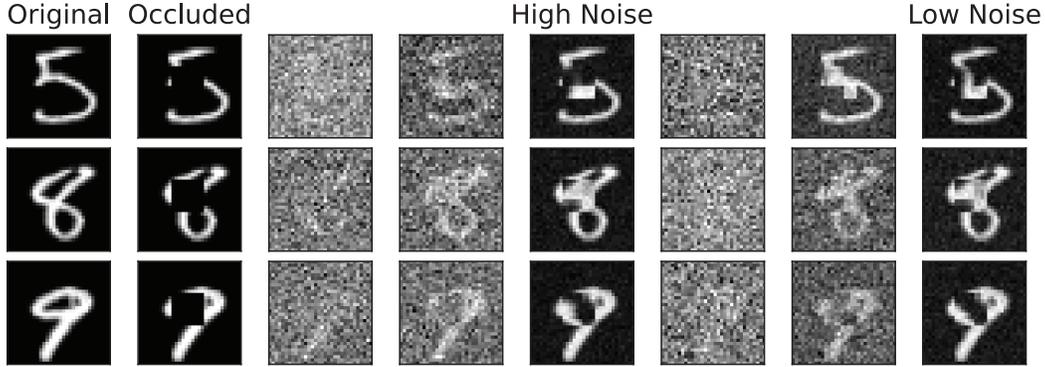


Figure 4: Resolving occlusion. A 15x15 black square occludes the digits in the first columns as shown in the second column. For high noise and low noise visual inference, the resolved digit is depicted in 5th and the last columns, respectively.

171 **3.2 FFA induces robustness to image noise and adversarial attacks**

172 Although in FFA training, we did not use any noise augmentation, as we show in this section, the
 173 network trained under FFA developed robustness to noise and adversarial attacks relative to the
 174 BP control. Previous works showed that BP networks are vulnerable to noise and highlighted that
 175 FA-trained networks are surprisingly robust (Goodfellow et al., 2015; Akrouf, 2019). When pixel
 176 noise was used to degrade input characters, we found that FFA was more robust than BP conferring
 177 some of the same robustness seen in FA (Figure 2 C). This advantage of FFA and FA over BP was
 178 also true for gradient-based white-box adversarial attacks (Figure Suppl. 8).

179 **4 Flexible visual inference through recursion**

180 While FFA is not explicitly a recurrent network, by coupling the feedforward and feedback pathways
 181 through mutual learning of dual, complementary losses, it may indirectly encourage compatibility
 182 in their inference processes. That is, we can run the network in a closed loop, passing z from the
 183 decoder back in as input to the encoder (replacing x) (see Figure 1). In this section, we explore
 184 the capabilities of FFA in dealing with missing information (noise or occlusion) and in generation
 185 (visual imagery, hallucinations, or dreams). It is worth noting that FFA was not trained to perform
 186 any of these tasks and was only trained for discrimination and reconstruction, conditioned on this
 187 discrimination.

188 The inference algorithm we use in this section relies on two main components: recursion, and noisiness
 189 of inference in each recursion. The algorithm was developed in Kadkhodaie and Simoncelli (2021)
 190 for denoiser autoencoders based on *Empirical Bayes Theorem* (Miyasawa, 1961). Although FFA is
 191 not trained as a denoiser autoencoder (no noisy input was used during training), we hypothesized that
 192 since it exhibits robustness to noise properties, then the theory applies here and the algorithm can be
 193 adapted to draw effective inferences from the representation learned by FFA. We especially focused
 194 on the effect of the noisiness of inference to inform the computational role of noise in neuronal
 195 activation as this remains largely unknown despite extensive active research (Echeveste and Lengyel,
 196 2018; Findling and Wyart, 2021; McDonnell and Ward, 2011).

197 **4.1 Denoising**

198 As a first step toward future recurrent processing within FFA, we simply ran the network in a closed
 199 loop, passing \hat{x} from the decoder back in as input to the encoder (replacing x) (see Figure 1) and
 200 found that both discrimination and reconstruction performance is sustained over iterations similar to
 201 an autoencoder whereas BP and FA discriminators change over multiple closed-loop iterations and
 202 thus would require a dynamic decoder to recover any performance (Figure 3).

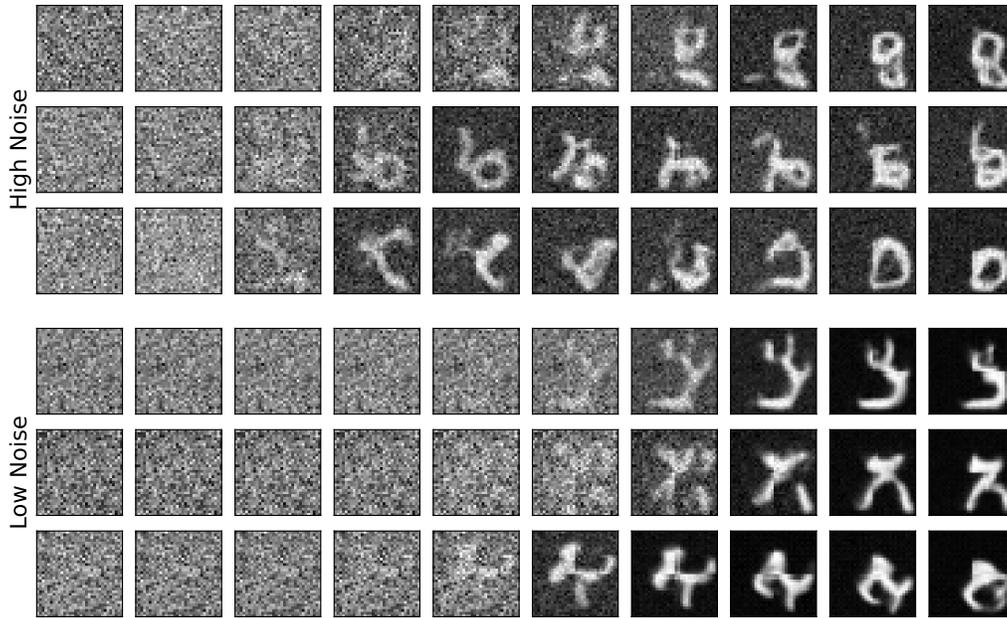


Figure 5: Hallucination. Without external input, we let the inference algorithm run on the FFA-trained network until convergence (the last column) for high noise (upper) and low noise (lower) inference. The sample iterations are linearly spaced and for high noise, there are typically twice as many iterations needed. Refer to Section 8.6 for iteration values.

203 4.2 Resolving occlusions

204 We occlude parts of an input image by a blank square and run the network inference. The assumption
 205 here is that the occluded image was briefly presented and during the inference, the original image is
 206 not accessible throughout inference. Figure 4 shows examples of completion of the pattern using
 207 FFA. Even though for high noise inference more iterations were needed, the generated samples do
 208 not reflect any superiority compared to low noise inference which took fewer iterations to converge.

209 4.3 Hallucination

210 Visual hallucinations refer to the experience of perceiving objects or events even when there is no
 211 corresponding sensory stimulation that would typically give rise to such perceptions. As mentioned
 212 above, the spontaneous activity in V1 is linked to the vividness of hallucinated patterns. Here, we
 213 let the FFA-trained network run through the inference algorithm starting from Gaussian noise and
 214 adding noise in each iteration. As shown in Figure 5, when in the high noise regime ($\beta = 0.2$), the
 215 quality of hallucinated digits is better compared to the low noise regime ($\beta = 0.99$, for the definition
 216 of β see Section 8.4). Given that the noise in the inference algorithm controls the convergence rate
 217 (Kadkhodaie and Simoncelli, 2021), these results suggest that the computational role of spontaneous
 218 activity in generating stronger hallucinated percepts may be the refinement of the hallucinated
 219 patterns.

220 4.4 Mental imagery

221 Visual mental imagery refers to the ability to create mental representations or pictures of visual
 222 information in the absence of actual sensory input (Pearson et al., 2015; Colombo, 2012). A key
 223 distinction between mental imagery and hallucinations is that mental imagery involves *voluntarily*
 224 creating mental images through imagination, while hallucinations are involuntary sensory perceptions.
 225 To implement the voluntary, top-down activation of a percept (e.g. '9'), we add the average activation
 226 pattern of the category in the latent layer to each recursion in the inference algorithm. Presumably, the
 227 brain has a recollection of the category which can be read out from memory during mental imagery.
 228 Figure 6 shows that as noise in the inference goes higher, so does the quality of the imagined digits.

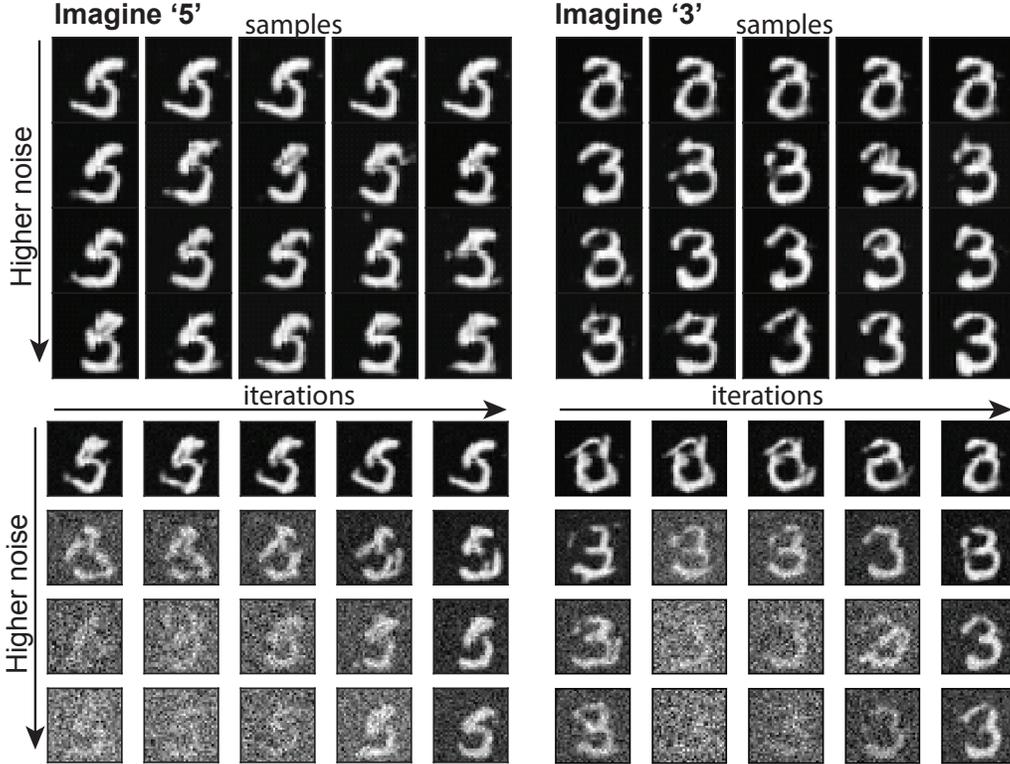


Figure 6: Visual imagery. Generated samples (upper panels) using the inference algorithm on the FFA-trained network when top-down signal '5' (left) and '3' (right) was activated. The sample iterations (equally spaced) for sample generations were shown in the lower panel. Each row corresponds to an inference noise level. Refer to Section 8.5 for iteration and β values

229 5 Limitations

230 We acknowledge several limitations of the Feedback-Feedforward Alignment (FFA) framework in its
 231 current form. One key limitation is the difficulty of scaling FFA to larger datasets, such as ImageNet.
 232 While we observed gaps in performance compared to classical backpropagation (BP) on CIFAR10,
 233 we found little difference compared to the Feedback Alignment (FA) baseline in discrimination
 234 performance. However, it is possible that FFA could be more suitable for specific architectures,
 235 such as transformers, where layer sizes do not decrease towards the output layer. Scaling up FFA
 236 requires further theoretical and empirical exploration. Another limitation is related to the assessment
 237 of the generated inferences. Currently, the evaluation relies primarily on visual inspection. Although
 238 we included classifier accuracy reports for denoising, it assumes that perception arises solely from
 239 top activations and that bottom hierarchy activation (such as V1) does not directly contribute to
 240 perception. Enhancing the evaluation methodology to incorporate more objective measures and
 241 quantitative assessments of generated inferences would strengthen the framework. Furthermore,
 242 while FFA demonstrates a balance between discrimination performance, efficient learning, and robust
 243 recurrent inference, it is important to acknowledge that FFA may not fully capture all aspects of the
 244 biological brain. The framework represents a step towards understanding the brain's mechanisms
 245 but may still fall short in faithfully replicating the intricacies of neural processing. Overall, these
 246 limitations highlight the need for further research and development to address the scalability of
 247 FFA, refine evaluation methodologies, and gain deeper insights into the biological plausibility of the
 248 framework. Overcoming these limitations will pave the way for more effective and robust alternatives
 249 to BP, advancing the understanding and application of neural network training algorithms.

250 **6 Conclusions**

251 In moving beyond classical error backpropagation training of a single-objective, feedforward network,
252 we have presented a feedforward-feedback algorithm that trains neural networks to achieve mutualistic
253 optimization of dual objectives. Co-optimization provides attendant advantages: avoids weight
254 transport, increases robustness to noise and adversarial attack, and gives feedback its own runtime
255 function that allows closed-loop inference. Through our experiments, we demonstrated that the
256 network trained using the FFA approach supports various visual inference tasks.

257 **7 Broader Impacts**

258 This work has broader impacts that include advancing our understanding of human perception,
259 enhancing the robustness and performance of neural networks, helping to identify the emergence
260 of closed-loop inference in larger networks for real-time applications, and potential implications
261 for clinical research of mental disorders. By studying the neural mechanisms underlying visual
262 perception, this research contributes to our understanding of natural and artificial vision.

263 **References**

- 264 Abid, H., Ahmad, F., Lee, S. Y., Park, H. W., Im, D., Ahmad, I., and Chaudhary, S. U. (2016). A
265 functional magnetic resonance imaging investigation of visual hallucinations in the human striate
266 cortex. *Behav. Brain Funct.*, 12(1):31.
- 267 Akrouf, M. (2019). On the Adversarial Robustness of Neural Networks without Weight Transport.
268 *arXiv:1908.03560 [cs, stat]*. arXiv: 1908.03560.
- 269 Akrouf, M., Wilson, C., Humphreys, P. C., Lillicrap, T., and Tweed, D. (2019). Deep Learning
270 without Weight Transport. *arXiv:1904.05391 [cs, stat]*. arXiv: 1904.05391.
- 271 Bartunov, S., Santoro, A., Richards, B. A., Marris, L., Hinton, G. E., and Lillicrap, T. (2018).
272 Assessing the Scalability of Biologically-Motivated Deep Learning Algorithms and Architectures.
273 *arXiv:1807.04587 [cs, stat]*. arXiv: 1807.04587.
- 274 Bengio, Y. (2014). How Auto-Encoders Could Provide Credit Assignment in Deep Networks via
275 Target Propagation. *arXiv:1407.7906 [cs]*. arXiv: 1407.7906.
- 276 Clark, A. (2013). Whatever next? predictive brains, situated agents, and the future of cognitive
277 science. *Behav. Brain Sci.*, 36(3):181–204.
- 278 Colombo, B. (2012). Mental imagery. In *Encyclopedia of the Sciences of Learning*, pages 2187–2191.
279 Springer US, Boston, MA.
- 280 Debes, S. R. and Dragoi, V. (2023). Suppressing feedback signals to visual cortex abolishes attentional
281 modulation. *Science*, 379(6631):468–473.
- 282 Dijkstra, N., Bosch, S. E., and van Gerven, M. A. J. (2017). Vividness of visual imagery depends on
283 the neural overlap with perception in visual areas. *J. Neurosci.*, 37(5):1367–1373.
- 284 Echeveste, R. and Lengyel, M. (2018). The redemption of noise: Inference with neural populations.
285 *Trends Neurosci.*, 41(11):767–770.
- 286 Findling, C. and Wyart, V. (2021). Computation noise in human learning and decision-making: origin,
287 impact, function. *Curr. Opin. Behav. Sci.*, 38:124–132.
- 288 Friston, K. (2009). The free-energy principle: a rough guide to the brain? *Trends Cogn. Sci.*,
289 13(7):293–301.
- 290 Ganis, G., Thompson, W. L., and Kosslyn, S. M. (2004). Brain areas underlying visual mental
291 imagery and visual perception: an fMRI study. *Cognitive Brain Research*, 20(2):226–241.
- 292 Gilbert, C. D. and Sigman, M. (2007). Brain states: top-down influences in sensory processing.
293 *Neuron*, 54(5):677–696.

- 294 Goodfellow, I. J., Shlens, J., and Szegedy, C. (2015). Explaining and Harnessing Adversarial
295 Examples. *arXiv:1412.6572 [cs, stat]*. arXiv: 1412.6572.
- 296 Grossberg, S. (1987). Competitive learning: From interactive activation to adaptive resonance.
297 *Cognitive Science*, 11(1):23–63.
- 298 He, K., Zhang, X., Ren, S., and Sun, J. (2015). Deep Residual Learning for Image Recognition.
299 *arXiv:1512.03385 [cs]*. arXiv: 1512.03385.
- 300 Helmholtz, H. v., Gullstrand, A., Kries, J. v., Nagel, W. A., and University College, L. L. S. (1909).
301 *Handbuch der Physiologischen Optik [electronic resource]*. Hamburg ; Leipzig : verlag von
302 Leopold Voss.
- 303 Kadhodaie, Z. and Simoncelli, E. (2021). Stochastic solutions for linear inverse problems using
304 the prior implicit in a denoiser. In Ranzato, M., Beygelzimer, A., Dauphin, Y., Liang, P., and
305 Vaughan, J. W., editors, *Advances in Neural Information Processing Systems*, volume 34, pages
306 13242–13254. Curran Associates, Inc.
- 307 Kar, K., Kubilius, J., Schmidt, K., Issa, E. B., and DiCarlo, J. J. (2019). Evidence that recurrent
308 circuits are critical to the ventral stream’s execution of core object recognition behavior. *Nat.*
309 *Neurosci.*, 22(6):974–983.
- 310 Keller, G. B. and Mrsic-Flogel, T. D. (2018). Predictive Processing: A Canonical Cortical Computa-
311 tion. *Neuron*, 100(2):424–435.
- 312 Khaligh-Razavi, S.-M. and Kriegeskorte, N. (2014). Deep supervised, but not unsupervised, models
313 may explain IT cortical representation. *PLoS Comput. Biol.*, 10(11):e1003915.
- 314 Kietzmann, T. C., Spoerer, C. J., Sörensen, L. K. A., Cichy, R. M., Hauk, O., and Kriegeskorte,
315 N. (2019). Recurrence is required to capture the representational dynamics of the human visual
316 system. *Proc. Natl. Acad. Sci. U. S. A.*, 116(43):21854–21863.
- 317 Kreiman, G. and Serre, T. (2020). Beyond the feedforward sweep: feedback computations in the
318 visual cortex. *Ann. N. Y. Acad. Sci.*, 1464(1):222–241.
- 319 Krizhevsky, A., Sutskever, I., and Hinton, G. E. (2012). ImageNet Classification with Deep Convolu-
320 tional Neural Networks. In Pereira, F., Burges, C. J. C., Bottou, L., and Weinberger, K. Q., editors,
321 *Advances in Neural Information Processing Systems 25*, pages 1097–1105. Curran Associates, Inc.
- 322 Kunin, D., Bloom, J. M., Goeva, A., and Seed, C. (2019). Loss Landscapes of Regularized Linear
323 Autoencoders. *arXiv:1901.08168 [cs, stat]*. arXiv: 1901.08168.
- 324 Kunin, D., Nayebi, A., Sagastuy-Brena, J., Ganguli, S., Bloom, J., and Yamins, D. L. K. (2020). Two
325 Routes to Scalable Credit Assignment without Weight Symmetry. *arXiv:2003.01513 [cs, q-bio,*
326 *stat]*. arXiv: 2003.01513.
- 327 Lee, D.-H., Zhang, S., Fischer, A., and Bengio, Y. (2014). Difference Target Propagation.
328 *arXiv:1412.7525 [cs]*. arXiv: 1412.7525.
- 329 Lee, T. S. and Mumford, D. (2003). Hierarchical bayesian inference in the visual cortex. *JOSA A*,
330 20(7):1434–1448.
- 331 Lillicrap, T. P., Cownden, D., Tweed, D. B., and Akerman, C. J. (2016). Random synaptic feedback
332 weights support error backpropagation for deep learning. *Nature Communications*, 7:13276.
- 333 Lillicrap, T. P. and Santoro, A. (2019). Backpropagation through time and the brain. *Current Opinion*
334 *in Neurobiology*, 55:82–89.
- 335 Lindsay, G. W. (2021). Convolutional neural networks as a model of the visual system: Past, present,
336 and future. *J. Cogn. Neurosci.*, 33(10):2017–2031.
- 337 Markov, N. T., Ercsey-Ravasz, M., Essen, D. C. V., Knoblauch, K., Toroczkai, Z., and Kennedy, H.
338 (2013). Cortical High-Density Counterstream Architectures. *Science*, 342(6158):1238406.

- 339 Markov, N. T., Vezoli, J., Chameau, P., Arnaud Falchier, Quilodran, R., Huissoud, C., Lamy, C.,
340 Misery, P., Giroud, P., Ullman, S., Barone, P., Dehay, C., Knoblauch, K., and Kennedy, H. (2014).
341 Anatomy of a hierarchy: Feedforward and feedback pathways in macaque visual cortex. *Journal*
342 *of Comparative Neurology*, 522(1):225–259.
- 343 McDonnell, M. D. and Ward, L. M. (2011). The benefits of noise in neural systems: bridging theory
344 and experiment. *Nat. Rev. Neurosci.*, 12(7):415–426.
- 345 Miyasawa, K. (1961). On the convergence of the learning process in a 2 x 2 non-zero-sum two-person
346 game.
- 347 Nayebi, A., Sagastuy-Brena, J., Bear, D. M., Kar, K., Kubilius, J., Ganguli, S., Sussillo, D., DiCarlo,
348 J. J., and Yamins, D. L. K. (2022). Recurrent connections in the primate ventral visual stream
349 mediate a trade-off between task performance and network size during core object recognition.
350 *Neural Comput.*, 34(8):1652–1675.
- 351 Pearson, J. (2019). The human imagination: the cognitive neuroscience of visual mental imagery.
352 *Nat. Rev. Neurosci.*, 20(10):624–634.
- 353 Pearson, J., Clifford, C. W. G., and Tong, F. (2008). The functional impact of mental imagery on
354 conscious perception. *Curr. Biol.*, 18(13):982–986.
- 355 Pearson, J., Naselaris, T., Holmes, E. A., and Kosslyn, S. M. (2015). Mental imagery: Functional
356 mechanisms and clinical applications. *Trends Cogn. Sci.*, 19(10):590–602.
- 357 Rao, R. P. N. and Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional
358 interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, 2(1):79–87.
- 359 Rumelhart, D. E., Hinton, G. E., and Williams, R. J. (1986). Learning representations by back-
360 propagating errors. *Nature*, 323(6088):533–536.
- 361 Semedo, J. D., Jasper, A. I., Zandvakili, A., Krishna, A., Aschner, A., Machens, C. K., Kohn, A.,
362 and Yu, B. M. (2022). Feedforward and feedback interactions between visual cortical areas use
363 different population activity patterns. *Nat. Commun.*, 13(1):1099.
- 364 Suzuki, K., Roseboom, W., Schwartzman, D. J., and Seth, A. K. (2017). A deep-dream virtual reality
365 platform for studying altered perceptual phenomenology. *Sci. Rep.*, 7(1):15982.
- 366 Suzuki, K., Seth, A. K., and Schwartzman, D. J. (2023). Modelling phenomenological differences in
367 aetiologically distinct visual hallucinations using deep neural networks.
- 368 Tang, H., Buia, C., Madhavan, R., Crone, N. E., Madsen, J. R., Anderson, W. S., and Kreiman, G.
369 (2014). Spatiotemporal dynamics underlying object completion in human ventral visual cortex.
370 *Neuron*, 83(3):736–748.
- 371 Tang, H., Schrimpf, M., Lotter, W., Moerman, C., Paredes, A., Ortega Caro, J., Hardesty, W., Cox,
372 D., and Kreiman, G. (2018). Recurrent computations for visual pattern completion. *Proc. Natl.*
373 *Acad. Sci. U. S. A.*, 115(35):8835–8840.
- 374 Walsh, K. S., McGovern, D. P., Clark, A., and O’Connell, R. G. (2020). Evaluating the neuro-
375 physiological evidence for predictive processing as a model of perception. *Ann. N. Y. Acad. Sci.*,
376 1464(1):242–268.
- 377 Yamins, D. L. K., Hong, H., Cadieu, C. F., Solomon, E. A., Seibert, D., and DiCarlo, J. J. (2014).
378 Performance-optimized hierarchical models predict neural responses in higher visual cortex. *Proc.*
379 *Natl. Acad. Sci. U. S. A.*, 111(23):8619–8624.

380 8 Supplementary

381 8.1 Model architectures

382 For the experiment on a fully connected architecture, we used a 4-layer network with [1024,
383 256,256,10] neurons in each layer and ReLU non-linearity between layers. For the experiment
384 on a convolutional architecture, we used a modified version of resnet (He et al., 2015), where the
385 last convolutional layer has the same number of channels as classes, and an adaptive average pooling
386 operator is used to read out of each channel (see below). Since the last layer doesn't have any
387 learnable parameters, the penultimate layer can be as large as desired which works fine for FFA. The
388 convolutional architecture consists of 11 convolutional layers with 658,900 trainable parameters in
389 total.

390 For autoencoder controls (trained under BP or FA), we additionally trained a linear decoder on the
391 activations of the penultimate layer to assess the linear separability of the representation learned by
392 autoencoders.

```
393 modelF: DataParallel(  
394   (module): AsymResLNet10F(  
395     (conv1): AsymmetricFeedbackConv2d(1, 64, kernel_size=(7, 7),  
396       stride=(2, 2), padding=(3, 3), bias=False)  
397     (bn1): BatchNorm2d(64, eps=1e-05, momentum=0.1,  
398       affine=True, track_running_stats=False)  
399     (relu): ReLU(inplace=True)  
400     (conv11): AsymmetricFeedbackConv2d(64, 64, kernel_size=(3, 3),  
401       stride=(1, 1), padding=(1, 1), bias=False)  
402     (bn11): BatchNorm2d(64, eps=1e-05, momentum=0.1,  
403       affine=True, track_running_stats=False)  
404     (conv12): AsymmetricFeedbackConv2d(64, 64, kernel_size=(3, 3),  
405       stride=(1, 1), padding=(1, 1), bias=False)  
406     (bn12): BatchNorm2d(64, eps=1e-05, momentum=0.1,  
407       affine=True, track_running_stats=False)  
408     (conv21): AsymmetricFeedbackConv2d(64, 64, kernel_size=(3, 3),  
409       stride=(1, 1), padding=(1, 1), bias=False)  
410     (bn21): BatchNorm2d(64, eps=1e-05, momentum=0.1,  
411       affine=True, track_running_stats=False)  
412     (conv22): AsymmetricFeedbackConv2d(64, 128,  
413       kernel_size=(3, 3),  
414       stride=(1, 1), padding=(1, 1), bias=False)  
415     (bn22): BatchNorm2d(128, eps=1e-05, momentum=0.1,  
416       affine=True, track_running_stats=False)  
417     (downsample1): AsymmetricFeedbackConv2d(64, 128,  
418       kernel_size=(1, 1), stride=(1, 1), bias=False)  
419     (bn23): BatchNorm2d(128, eps=1e-05, momentum=0.1,  
420       affine=True, track_running_stats=False)  
421     (conv31): AsymmetricFeedbackConv2d(128, 128,  
422       kernel_size=(3, 3),  
423       stride=(2, 2), padding=(1, 1), bias=False)  
424     (bn31): BatchNorm2d(128, eps=1e-05, momentum=0.1,  
425       affine=True, track_running_stats=False)  
426     (conv32): AsymmetricFeedbackConv2d(128, 128,  
427       kernel_size=(3, 3),  
428       stride=(1, 1), padding=(1, 1), bias=False)  
429     (bn32): BatchNorm2d(128, eps=1e-05, momentum=0.1,  
430       affine=True, track_running_stats=False)  
431     (conv41): AsymmetricFeedbackConv2d(128, 128,  
432       kernel_size=(3, 3),  
433       stride=(1, 1), padding=(1, 1), bias=False)  
434     (bn41): BatchNorm2d(128, eps=1e-05, momentum=0.1,  
435       affine=True, track_running_stats=False)
```

```

436     (conv42): AsymmetricFeedbackConv2d(128, 10,
437     kernel_size=(3, 3),
438     stride=(1, 1), padding=(1, 1), bias=False)
439     (bn42): BatchNorm2d(10, eps=1e-05, momentum=0.1,
440     affine=True, track_running_stats=False)
441     (downsample2): AsymmetricFeedbackConv2d(128, 10,
442     kernel_size=(1, 1), stride=(2, 2), bias=False)
443     (avgpool): AdaptiveAvgPool2d(output_size=(1, 1))
444 )
445
446 modelB: DataParallel(
447     (module): AsymResLNet10B(
448     (upsample2): AsymmetricFeedbackConvTranspose2d(10, 128,
449     kernel_size=(1, 1), stride=(2, 2), output_padding=(1, 1),
450     bias=False)
451     (bn42): BatchNorm2d(10, eps=1e-05, momentum=0.1,
452     affine=True, track_running_stats=False)
453     (conv42): AsymmetricFeedbackConvTranspose2d(10, 128,
454     kernel_size=(3, 3), stride=(1, 1), padding=(1, 1), bias=False)
455     (relu): ReLU(inplace=True)
456     (bn41): BatchNorm2d(128, eps=1e-05, momentum=0.1,
457     affine=True, track_running_stats=False)
458     (conv41): AsymmetricFeedbackConvTranspose2d(128, 128,
459     kernel_size=(3, 3), stride=(1, 1), padding=(1, 1), bias=False)
460     (bn32): BatchNorm2d(128, eps=1e-05, momentum=0.1,
461     affine=True, track_running_stats=False)
462     (conv32): AsymmetricFeedbackConvTranspose2d(128, 128,
463     kernel_size=(3, 3), stride=(1, 1), padding=(1, 1), bias=False)
464     (bn31): BatchNorm2d(128, eps=1e-05, momentum=0.1,
465     affine=True, track_running_stats=False)
466     (conv31): AsymmetricFeedbackConvTranspose2d(128, 128,
467     kernel_size=(3, 3), stride=(2, 2), padding=(1, 1),
468     output_padding=(1, 1), bias=False)
469     (bn23): BatchNorm2d(128, eps=1e-05, momentum=0.1,
470     affine=True, track_running_stats=False)
471     (upsample1): AsymmetricFeedbackConvTranspose2d(128, 64,
472     kernel_size=(1, 1), stride=(1, 1), bias=False)
473     (bn22): BatchNorm2d(128, eps=1e-05, momentum=0.1,
474     affine=True, track_running_stats=False)
475     (conv22): AsymmetricFeedbackConvTranspose2d(128, 64,
476     kernel_size=(3, 3), stride=(1, 1), padding=(1, 1), bias=False)
477     (bn21): BatchNorm2d(64, eps=1e-05, momentum=0.1,
478     affine=True, track_running_stats=False)
479     (conv21): AsymmetricFeedbackConvTranspose2d(64, 64,
480     kernel_size=(3, 3), stride=(1, 1), padding=(1, 1), bias=False)
481     (bn12): BatchNorm2d(64, eps=1e-05, momentum=0.1,
482     affine=True, track_running_stats=False)
483     (conv12): AsymmetricFeedbackConvTranspose2d(64, 64,
484     kernel_size=(3, 3), stride=(1, 1), padding=(1, 1), bias=False)
485     (bn11): BatchNorm2d(64, eps=1e-05, momentum=0.1,
486     affine=True, track_running_stats=False)
487     (conv11): AsymmetricFeedbackConvTranspose2d(64, 64,
488     kernel_size=(3, 3), stride=(1, 1), padding=(1, 1), bias=False)
489     (bn1): BatchNorm2d(64, eps=1e-05, momentum=0.1,
490     affine=True, track_running_stats=False)
491     (conv1): AsymmetricFeedbackConvTranspose2d(64, 1,
492     kernel_size=(7, 7), stride=(2, 2), padding=(2, 2),
493     output_padding=(1, 1), bias=False))
494 )

```

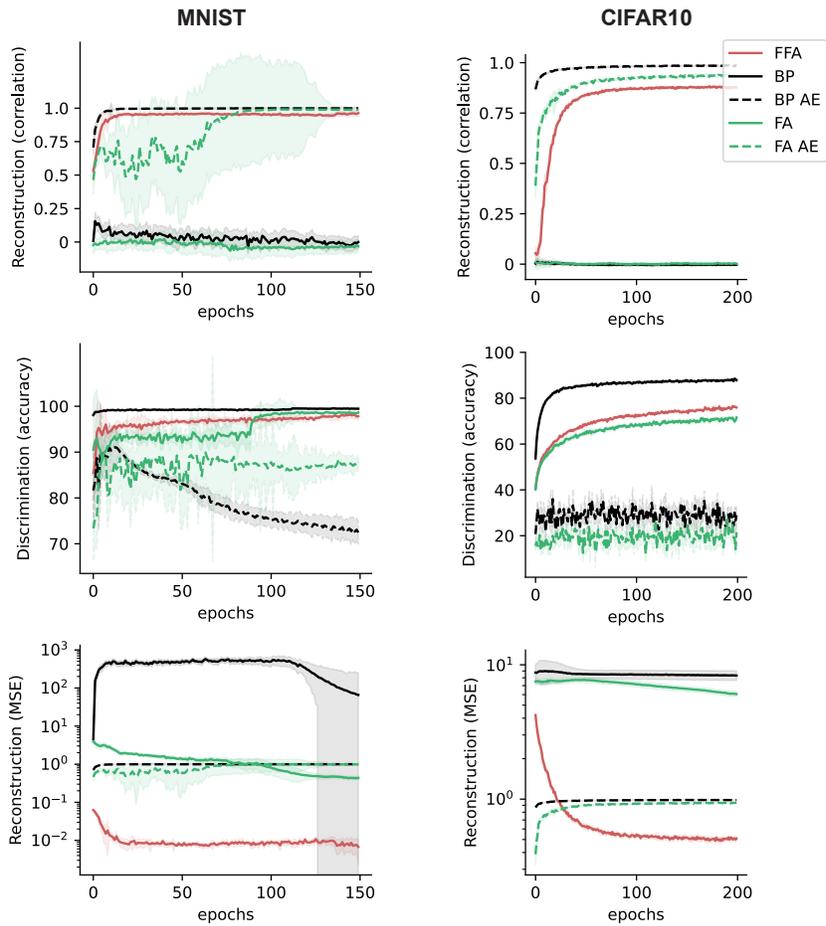


Figure 7: Co-optimization in FFA compared to single objective (either discrimination or reconstruction) control networks for MNIST and CIFAR10 (extensive version of Figure 2).

496 **8.3 Robustness assessment**

497 We added Gaussian noise with zero mean and varied the variance $\sigma^2 = [0.0, 0.2, 0.4, 0.8, 1.0]$ to
 498 assess the robustness of models to input noise. We also performed a widely used white box adversarial
 499 attack Fast Gradient Sign Method (FGSM) (Goodfellow et al., 2015). FGSM can be summarized by

$$x' = x + \sigma \text{sign}(\Delta_x J(x, y^*))$$

500 where σ is the magnitude of the perturbation, J is the loss function and y^* is the label of x . While in
 501 BP this perturbation is computed through transposed forward parameters, for FFA and FA, we use
 502 their gradient pass parameters which are learned feedback and random feedback, respectively. We
 used a range of ϵ to cover the interval between 0 to 1.

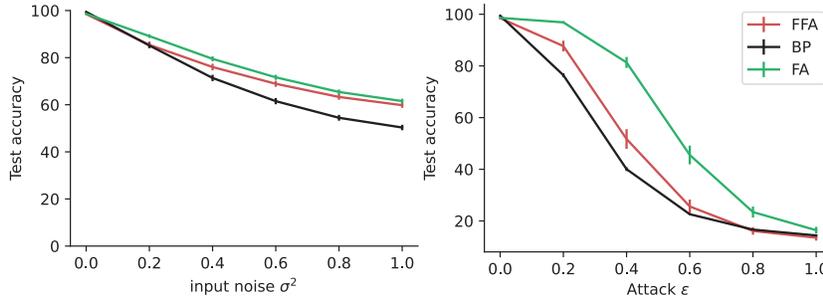


Figure 8: Robustness to Gaussian noise and adversarial attacks for MNIST. Robustness to noise and adversarial attacks in input (image) space for FFA and control algorithms. FA and FFA both exhibit more robustness than BP-trained discriminators.

503

504 **8.4 Visual inference algorithm**

505 We adapt the sampling algorithm developed in (Kadkhodaie and Simoncelli, 2021) to implement the
 506 visual inference in FFA-trained networks. β parameter which varies between 0 and 1 controls the
 507 proportion of injected noise ($\beta = 1$ indicates no noise).

Algorithm 1 *

parameters: $\sigma_0, \sigma_L, h_0, \beta$
 initialization: $t = 1$, draw $x_0 \sim \mathcal{N}(0.5, \sigma_0^2 I)$
while $\sigma_{t-1} \leq \sigma_L$ **do**
 $h_t = \frac{h_0 t}{1 + h_0(t-1)}$
 $d_t = x_{t-1} - \hat{x}_{t-1}$
 $\sigma_t^2 = \frac{\|d_t\|^2}{N}$
 $\gamma_t^2 = ((1 - \beta h_t)^2 - (1 - h_t)^2) \sigma_t^2$
 Draw $z_t \sim \mathcal{N}(0, I)$
 $x_t \leftarrow x_{t-1} + h_t d_t + \gamma_t z_t$
 $t \leftarrow t + 1$
end

Stochastic gradient ascent method for sampling from the implicit prior in a denoiser autoencoder as in Kadkhodaie and Simoncelli (2021)

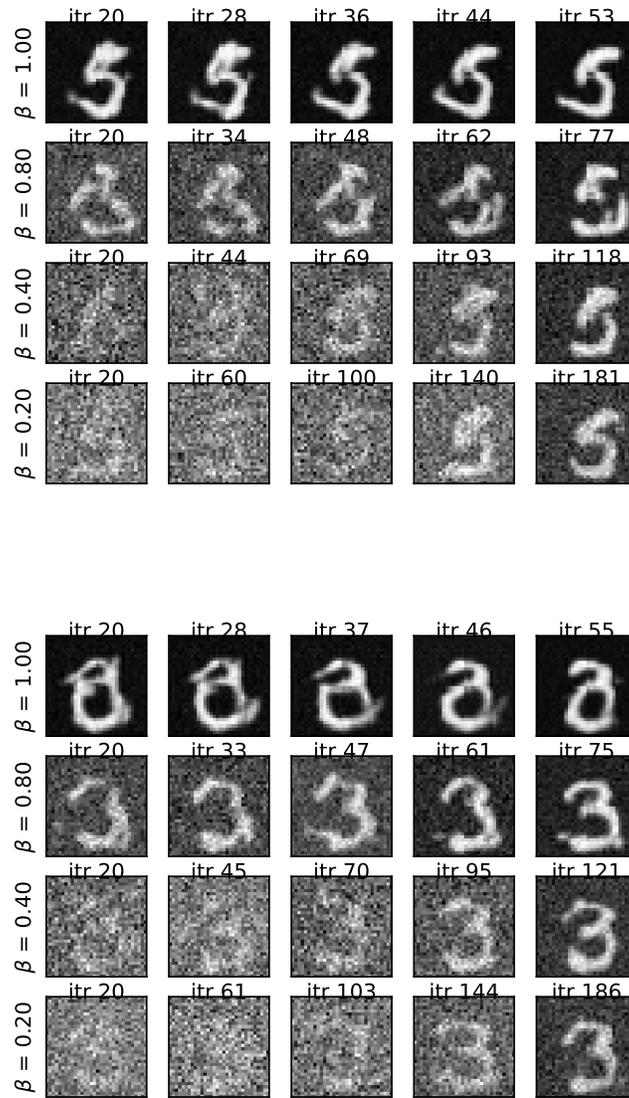


Figure 9: Sample visual imagery related to Figure 6 in the main text.

509 **8.6 Hallucinations**

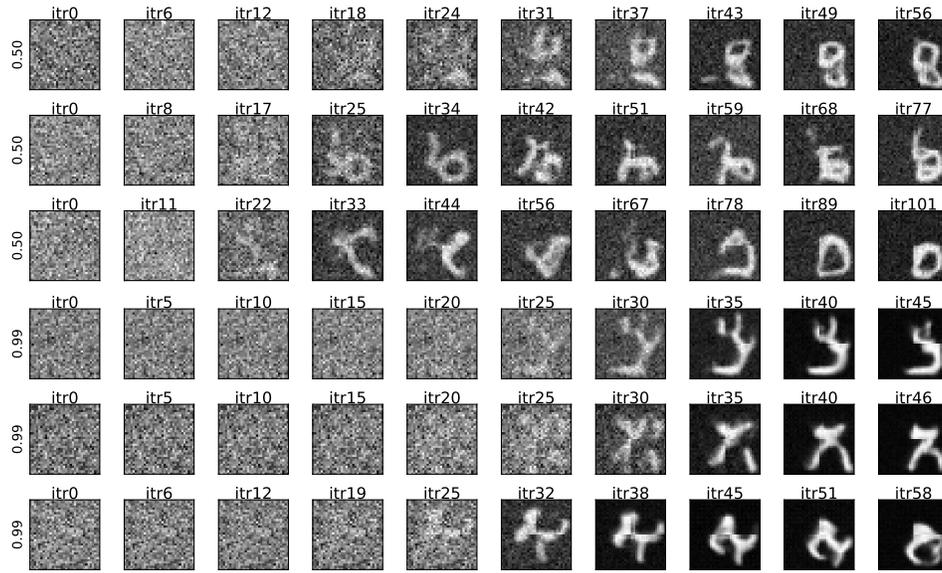


Figure 10: Sample hallucinations related to Figure 5 in the main text.