Neural heterogeneity promotes robust learning

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The brain is a hugely diverse, heterogeneous structure. Whether or not heterogeneity at the neural level plays a functional role remains unclear, and has been relatively little explored in models which are often highly homogeneous. We compared the performance of spiking neural networks trained to carry out tasks of real-world difficulty, with varying degrees of heterogeneity, and found that heterogeneity substantially improved task performance. Learning with heterogeneity was more stable and robust, particularly for tasks with a rich temporal structure. In addition, the distribution of neuronal parameters in the trained networks is similar to those observed experimentally. We suggest that the heterogeneity observed in the brain may be more than just the byproduct of noisy processes, but rather may serve an active and important role in allowing animals to learn in changing environments.
The brain is known to be deeply heterogeneous at all scales, but it is still not known whether this heterogeneity plays an important functional role or if it is just a byproduct of noisy developmental processes and contingent evolutionary history. A number of hypothetical roles have been suggested (reviewed in ref. 2), including in efficient coding9–10, reliability11, working memory12, and functional specialisation13. However, previous studies have largely used simplified tasks or networks, and it remains unknown whether or not heterogeneity can help animals solve complex information processing tasks in natural environments. Recent work has allowed us, for the first time, to train biologically realistic spiking neural networks to carry out these tasks at a high level of performance, using methods derived from machine learning. We used two different learning models3,14 to investigate the effect of introducing heterogeneity in the time scales of neurons when performing tasks with realistic and complex temporal structure. We found that it improves the overall performance, makes learning more stable and robust, and that the network learns neural parameter distributions that match experimental observations, suggesting that the heterogeneity observed in the brain may be a vital component of its ability to adapt to new environments.

Results
Time scale heterogeneity improves learning on tasks with rich temporal structure. We investigated the role of neural heterogeneity in task performance by training recurrent spiking neural networks to classify visual and auditory stimuli with varying degrees of temporal structure. The model used three layers of spiking neurons: an input layer, a recurrently connected layer, and a readout layer used to generate predictions (Fig. 1A), a widely used minimal architecture (e.g. Maass et al.15, Neftci et al.14). Heterogeneity was introduced by giving each neuron an individual membrane and synaptic time constant. We compared four different conditions: initial values could be either homogeneous or heterogeneous, and training could be either standard or heterogeneous (Fig. 1B). In more detail, time constants were either initialised with a single value (homogeneous initialisation), or randomly according to a gamma distribution (heterogeneous initialisation). In both types of training, the parameters of the models were optimised using surrogate gradient descent14. Synaptic weights were trainable in both standard and heterogeneous training regimes, while time constants were either held fixed at their initial values in the standard training regime, or could be modified in the heterogeneous training regime.

We used five different datasets with varying degrees of temporal structure. Neuromorphic MNIST (N-MNIST)16, Fashion-MNIST (F-MNIST)17, and the DVS128 Gesture dataset18 feature visual stimuli, while the Spiking Heidelberg Digits (SHD) and Spiking Speech Commands (SSC) datasets19 are auditory. N-MNIST and DVS128 use a neuromorphic vision sensor to generate spiking activity, by moving the sensor with a static visual image of handwritten digits (N-MNIST) or by recording humans making hand gestures (DVS128). F-MNIST is a dataset of static images that are widely used in machine learning, which we converted into spike times by treating the image intensities as input currents to model neurons, so that higher intensity pixels would lead to earlier spikes, and lower intensity to later spikes. Both SHD and SSC use the same detailed model of the activity of bushy cells in the cochlear nucleus developed in Cramer et al.19, in response to spoken digits (SHD) or commands (SSC). Their model consists of standard components from the auditory modelling literature, including a hydrodynamic basilar membrane, transmitter pool and inhomogeneous Poisson process hair cell, and leaky integrate-and-fire bushy cell. Of these datasets, N-MNIST and F-MNIST have minimal temporal structure, as they are generated from static images. DVS128 has some temporal structure as it is recorded motion, but it is possible to perform well at this task by discarding the temporal information. The auditory tasks SHD and SSC by contrast have very rich temporal structure. In all cases, we used the train/test split suggested by the corresponding dataset authors to compare our performance with previous baselines fairly.

We found that heterogeneity in time constants had a profound impact on performance on those training datasets where information was encoded in the precise timing of input spikes (Table 1 and Fig. 2A). On the most temporally complex auditory tasks, accuracy improved by a factor of around 15–20%, while for the least temporally complex task N-MNIST, we saw no improvement at all. For the gesture dataset DVS128, we can identify the source of the (intermediate) improvement as the heterogeneous models being better able to distinguish between spatially similar but temporally different gestures, such as clockwise and anticlockwise versions of the same gesture (Supplementary Fig. 7A, B). This suggests that we might see greater improvements for a richer version of this dataset in which temporal structure was more important.

We verified that our results were due to heterogeneity and not simply to a better tuning of time constants in two ways. Firstly, we performed a grid search across all homogeneous time constants for the SHD dataset and used the best values for our comparison. Secondly, we observe that the distribution of time constants after training is very similar and heterogeneous regardless of whether it was initialised with a homogeneous or heterogeneous distribution (Fig. 2B), indicating that the heterogeneous distribution is optimal.

Introducing heterogeneity allows for a large increase in performance at the cost of only a very small increase in the number of parameters (0.23% for SHD, because we have added some neuron-specific parameters, but not added any synapse-specific ones, and the vast majority of parameters are synaptic weights), and without using any additional neurons or synapses. Heterogeneity is therefore a metabolically efficient strategy. It is also a computationally efficient strategy of interest to neuromorphic computing, because adding heterogeneous time constants to the model adds $O(n)$ to memory use and computation time when simulating the model, while adding more neurons adds $O(n^2)$ (because the model is fully connected, so the number of synaptic weights is proportional to the square of the number of neurons).

Note that it is possible to obtain better performance using a larger number of neurons. For example, Cramer et al.19 obtained a performance of 83.2% on the SHD dataset without heterogeneity using 1024 neurons and data augmentation techniques, whereas we obtained 82.7% using 128 neurons and no data augmentation. We focus on smaller networks here for two reasons. Firstly, we wanted to systematically investigate the effect of different training regimes, and the current limitations of surrogate gradient descent mean that each training session takes several days. Secondly, with larger numbers of neurons, performance even without heterogeneity can in some cases approach the ceiling on these tasks (which are still simple in comparison to those faced by animals in real environments), making it more difficult to see the effect of different architectures. In the case of the SSC dataset, however, even with this limitation to small networks, heterogeneity confers such an advantage that our results are state of the art (for spiking neural networks) by a large margin.

We also tested the effect of introducing heterogeneity of other neuron parameters, such as the firing threshold and reset potential, but found that it made no appreciable difference. This
was because for our model, changing these is almost equivalent to a simple scaling of the membrane potential variable. By contrast, Bellec et al.\textsuperscript{24} found that introducing an adaptive threshold did improve performance, presumably because it allows for much richer temporal dynamics (in line with earlier findings\textsuperscript{25}).

Predicted time constant distributions match experimental data. In all our tasks, the distributions of time constants after training approximately but not exactly fit a log-normal or gamma distribution (with different parameters for each task). They are also consistent across different training runs (Supplementary Figs. 1 and 2) and initial distributions (Supplementary Figs. 8 and 9), suggesting that the learned distributions may be optimal.

Using publicly available datasets including time constants recorded in large numbers of neurons in different animals and brain regions\textsuperscript{20–23}, we found similar distributions to those we predicted (Fig. 2C). This is striking, as our model is optimised for a single, relatively simple task, while animals in real environments face a range of tasks, each of which is more difficult than our model tasks. The parameters for the experimentally observed distributions are different for each animal and region, just as for different tasks in our simulations. Interestingly, the distribution parameters are also different for each cell type in the experimental data, a feature not replicated in our simulations as all cells are identical. This suggests that introducing further diversity in terms of different cell types may lead to even better performance.
Heterogeneity improves generalisation: speech learning across time scales. Sensory signals such as speech and motion can be recognised across a range of speeds by humans and animals. We tested the role of heterogeneity in learning a circuit that can function across a wide range of speeds. We augmented the SHD spoken digits datasets to include faster or slower versions of the samples, multiplying all spike times by a temporal scale as an extremely simplified model that captures a part of the difficulty of this task (Fig. 2D). During training, temporal scales were randomly selected from a distribution roughly matching human syllabic rate distributions. Heterogeneous initialisation results in a more stable and robust training trajectory for F-MNIST, leading to a better performance overall. In the first experiment, we took the augmented SHD spoken digits dataset from the previous section, selected the hyperparameters to give the best performance at a time scale of 1, but then trained and tested the network at a different time scale (Fig. 2F). We used training of weights only, since allowing retraining of time constants lets the network cancel out the effect of changing the time scale. With a homogeneous or narrow heterogeneous initial distribution (blue line in Fig. 2F), performance falls off for time scales far from the optimal one, particularly for larger time scales (slower stimuli). However, a wide heterogeneous initial distribution (purple line in Fig. 2F) allows for good performance across all time scales tested, at the cost of slightly lower peak performance.
performance at the best time scale. We tested whether or not this was solely due to the presence of a few neurons with long time constants by introducing an intermediate distribution where the majority of time constants were the same as the homogeneous case, with a small minority of much longer time constants (brown line in Fig. 2F). The performance of this distribution was intermediate between the homogeneous and heterogeneous distributions, a pattern that is repeated in our second experiment below.

In the second experiment, we switched to a very different learning paradigm, FORCE training of spiking neural networks\textsuperscript{13} to replay a learned signal, in this case, a recording of a zebra finch call (Fig. 3A; from Blättler and Hahnloser\textsuperscript{27}). This method does not allow for heterogeneous training (tuning time constants), so we only tested the role of untrained heterogeneous neuron parameters. We tested three configurations: fully homogeneous (single 20 ms time constant as in the original paper); intermediate, (each neuron randomly assigned a fixed fast 20 ms or slow 100 ms time constant); or fully heterogeneous (each neuron randomly assigned a time constant drawn from a gamma distribution).

Nicola and Clopath\textsuperscript{13} showed that network performance is highly dependent on two hyperparameters ($G$ and $Q$ in their paper). We, therefore, tuned these hyperparameters for a network of a fixed size ($N = 1000$ neurons) and ran the training and testing for networks of different sizes (Fig. 3B). As the network size started to diverge, the homogeneous network began to make large errors, while the fully heterogeneous network was able to give low errors for all network sizes. The intermediate network was able to function well across a wider range of network sizes, but still eventually failed for the largest network sizes. At these large network sizes, the homogeneous network neurons fire at or close to their maximal rate and training cannot take place, leading to poor performance (Fig. 3C). The robustness of the heterogeneous version of the network can be measured by the area of the hyperparameter space that leads to good performance (Fig. 3D). Adding partial or full heterogeneity leads to an improvement in learning for all points in the hyperparameter space, again suggesting that it can improve the robustness of learning in a wide range of situations.

**Discussion**

We trained spiking neural networks at difficult classification tasks, either forcing all neuron time constants to be the same (homogeneous) or allowing them to be different (heterogeneous). We found that introducing heterogeneity improved the overall performance across a range of tasks and training methods, but particularly so on tasks with richer intrinsic temporal structure. Learning was more robust, for heterogeneous networks, in that the networks were able to learn across a range of different environments, and when the hyperparameters of learning were mistuned. When the learning rule was allowed to tune the time

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**Fig. 3 Robustness to learning hyperparameter mistuning.** A Spectrogram of a zebra finch call. The network has to learn to reproduce this spectrogram, chosen for its spectrotemporal complexity. B Error for three networks at different network sizes (hyperparameters $G$ and $Q$ were chosen to optimise performance at $N = 1000$ neurons as given in Table 4). Networks are fully homogeneous (Homog); intermediate, where each neuron is randomly assigned slow or fast dynamics (Double); or fully heterogeneous, where each neuron has a random time constant drawn from a gamma distribution (Gamma). C Raster plots of 50 neurons randomly chosen, and reconstructed spectrograms under fully homogeneous and fully heterogeneous (Gamma) conditions for $N = 4000$ neurons as indicated in B. D Reconstruction error. Each row is one of the three configurations shown as lines in B. Each column is a network size. The axes of each image give the learning hyperparameters ($G$ and $Q$). Grey pixels correspond to log mean square error above 0, corresponding to a complete failure to reconstruct the spectrogram. The larger the coloured region, the more robust the network is, and less tuning is required.
constants as well as synaptic weights, a consistent distribution of
time constants was found, akin to a log-normal or gamma dis-
tribution, and this qualitatively matched time constants measured
in experimental data. Our model is consistent with the two
possibilities that these time constant distributions are learned
during an individuals lifetime, or that they are found as a result of
an evolutionary process.

We conclude from this that neural heterogeneity is a meta-
bolically efficient strategy for the brain. Heterogeneous networks
have no additional cost in terms of the number of neurons or
synapses, and perform as well as homogeneous networks which
have an order of magnitude more neurons. This gain also extends
to neuromorphic computing systems, as adding heterogeneity to
the neuron model adds an additional time and memory cost of
only $O(n)$, while adding more neurons has a cost of $O(n^2)$
(because all neurons are connected). Further, in some neuro-
morphic systems like BrainScaleS this heterogeneity is already
present as part of the manufacturing process. In addition to
their overall performance being better, heterogeneous networks
are more robust and able to learn across a wide range of environ-
ments, which is clearly ethologically advantageous. Again, this
has a corresponding benefit to neuromorphic computing and
potentially machine learning more generally, in that it reduces the
cost of hyperparameter tuning, which is often one of the largest
costs for developing these models.

We now turn to the matter of the extent of time constant
tuning in real nervous systems. It could be the case that the
heterogeneous distribution of time constants observed in different
animals and brain regions (Fig. 2C) is simply a product of noisy
developmental processes. We cannot rule this out. However, our
results show that the distributions observed experimentally clos-
ely match the optimal ones found by simulations, and this
optimal distribution confers a substantial computational advan-
tage. It, therefore, seems likely that the brain makes use of this
advantage. We found that any degree of heterogeneity improves
performance, but that the best performance could be found by
tuning the distribution of time constants to match the task.
Without a more detailed model of particular brain regions in
specific animals, and the real-world tasks they solve, it is difficult
to conclude whether or not the precise distributions observed
experimentally are tuned to those tasks or not. Further, having a
less precisely tuned distribution may lead to greater robustness in
uncertain environments.

A number of studies have used heterogeneous or tunable time
constants to model all our simulations. In this model, the membrane potential of the $r$th layer $\mathcal{U}_l^{(r)}(t)$ varies over time following Eq. (1).

$$
t_m \mathcal{U}_l^{(r)}(t) = -\left( \mathcal{U}_l^{(r)}(t) - U_r \right) + \mathcal{I}_l^{(r)}(t)
$$

Here, $t_m$ is the membrane time constant, $U_r$ is the resting potential and $\mathcal{I}_l^{(r)}(t)$ is the input current. When the membrane potential reaches the threshold value $\mathcal{U}_l^{(r)}$, a spike is emitted. $\mathcal{U}_l(t)$ resets to the reset potential $U_r$ and then enters a refractory period that lasts $t_m$ seconds where the neuron cannot spike.

Spikes emitted by the $r$th neuron in layer $l - 1$ at a finite set of times $\{t_s^{(r)}\}$ can be formalised as a spike train $S_l^{(r)}(t)$ defined as in Eq. (2)

$$
S_l^{(r)}(t) = \sum \delta(t - t_s^{(r)})
$$

The input current $\mathcal{I}_l^{(r)}(t)$ is obtained from the spike trains of all presynaptic neurons $j$ connected to neuron $i$ following Eq. (3)

$$
t_m \mathcal{I}_l^{(r)}(t) = -\mathcal{I}_l^{(r)}(t) + \sum_{j} \mathcal{W}_{ij}^{(r)} S_j^{(l)}(t) + \sum_{j} \mathcal{V}_{ij}^{(r)} S_l^{(r)}(t)
$$

We use the Leaky Integrate and Fire (LIF) neuron model in all our simulations. In this model, the membrane potential of the $r$th neuron in the $\lambda$th layer $\mathcal{U}_l^{(r)}(t)$ varies over time following Eq. (1). Constants, and it would be interesting to extend our methods to
networks with multiple cell types, including more biophysically
detailed cell models.

Our computational results show a compelling advantage for
heterogeneity, and this makes intuitive sense. Having hetero-
genous time constants in a layer allows the network to integrate
incoming spikes at different time scales, corresponding to shorter
or longer memory traces, thus allowing the readout layer to
capture information at several scales and represent a richer set of
functions. It would be very valuable to extend this line of thought
and find a rigorous theoretical explanation of the advantage of
heterogeneity.

### Methods

#### Neuronal and synaptic models

We use the Leaky Integrate and Fire (LIF) neuron model in all our simulations. In this model, the membrane potential of the $r$th neuron in the $\lambda$th layer $\mathcal{U}_l^{(r)}(t)$ varies over time following Eq. (1).

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a recurrent unit since it has access to its own previous state, different neurons in the same spiking layer will only be connected if any of the non-diagonal elements of $V^{(0)}$ is non-zero. In other words, all spiking neural networks (SNNs) built using this model are RNNs but not all RNNs are recurrent SNNs (RSNNs).

We can cascade I spiking layers to form a deep spiking neural network analogous to a conventional deep neural network and train it using gradient descent. However, as Eq. (6) is non-differentiable, we need to modify the backwards pass as in ref. 14 so that the backpropagation through time (BPTT) algorithm can be used to update the network parameters.

This means that while in the forward pass the network follows a step function as in Eq. (6), in the backwards pass it follows a sigmoidal function described in Eq. (7), with a steepness set by $\beta$.

We can now use gradient descent to optimise the synaptic weights $W^{(0)}$ and $V^{(0)}$ as in conventional deep learning. We can also optimise the spiking neuron-specific parameters $U_{sc}, U_{th}, U$ since they can be seen as bias terms. The time constants can also be indirectly optimised by training $\alpha$ and $\beta$, which can be seen as forgetting factors.

We apply a clipping function $\alpha$ and $\beta$ after every update.

\[
\text{clip}(x) = \begin{cases} 
  e^{-1/3} & \text{if } x < e^{-1/3} \\
  0.995 & \text{if } x > 0.995
\end{cases} 
\]

In order to ensure stability, the forgetting factors have to be $<1$. Otherwise, the current and membrane potential would grow exponentially. Secondly, to make the loss function $\mathcal{L}$ be convex, we define $\Delta t = \Delta t_{\text{min}}$, where $\Delta t_{\text{min}} = \min_{t} (\Delta t + 1/3)$. As for the upper bound, we chose a maximum time constant of 100 ms (corresponding to $\exp(-\Delta t_{\text{min}}) = 0.995$) informed by the time constants reported in the NeuroElectro database, which shows that about 99.5% of the membrane time constants recorded from biological neurons have time constants below this value. The lower bound is also consistent with this database given our simulation time step of 0.5 ms. Since there is no data available on synaptic time constants, we chose the same range as for the membrane constant. We also set clipping limits for $U_{sc}, U_{th}, U$, such that they are always between the ranges specified in Table 2.

There are several ways in which the neuron parameters may be trained. One possibility is to make all neurons in a layer share the same neuron parameters. That is, a single value of $U_{sc}, U_{th}, U, \alpha, \beta$ is trained and shared by all neurons in a layer. Another possibility is to optimise each of these parameters in each neuron individually as we have done in our experiments. We also always trained the weight matrices $W^{(0)}$ and $V^{(0)}$. Training was done by using automatic differentiation on PyTorch and Adam optimiser with a learning rate $10^{-3}$ and betas (0.9, 0.999).

In all surrogate gradient descent experiments, a single recurrent spiking layer with 128 neurons received all input spikes. This recurrent layer is followed by a feed-forward readout layer with $K$ set to in Table 2. In all surrogate gradient descent experiments, a single recurrent spiking layer with 128 neurons received all input spikes. This recurrent layer is followed by a feed-forward readout layer with $K$ set to in Table 2.

A gamma initialised synaptic time constants, we draw the different synaptic time constant values allowed of 100 ms. The aim of this was to test whether all that was needed was some neurons with a longer memory. We chose 5% since the optimal distribution of trained time constants in the SHD shows that about this fraction of neurons reach this maximum value.

All states $\mathbf{I}(0)$ and $\mathbf{U}(0)$ are initialised to 0. For the weights $W$ and $V$, we independently sampled from a uniform distribution $U(k^{-1/2}, k^{-1/2})$, with $k$ being the number of afferent connections.

**FORCE training.** The FORCE method is used to train a network consisting of a single recurrent layer of LIF neurons as in ref. 13. In particular, we followed the method used to learn to reproduce a songbird singing. In this method, there are no feed-forward weights and only the recurrent weights $V$ are trained. We can express these weights as $V = Gv + Q\eta^T$.

The first term in Eq. (10), namely $Gv$, remains static during training and it is initialised to set the network into chaotic spiking. The learned component of the weights $\phi^T \in \mathbb{R}^{K \times N}$ is updated using the Recursive Least Squares algorithm. The vector $\theta \in \mathbb{R}^{N \times K}$ serves as a decoder and it is static during learning. The constants $G$ and $Q$ govern the ratio between chaotic and learned weights.

With this definition of $V$, we can write the currents into the neurons as the sum $\mathbf{I}(t) = I_{\mathbf{I}}[t] + I_{\mathbf{r}}[t]$ (we dropped the layer $l$ subscript since we only have a single layer) where we define

\[
I_{\mathbf{I}}[t] = aL_{\mathbf{I}}[t] + GV[S][t] 
\]

\[
I_{\mathbf{r}}[t] = QI_{\mathbf{r}}^T \theta R[t] 
\]

\[
r[t] + \mu = \eta \theta^T \theta r[t] + S[t] 
\]

In order to stabilise the network dynamics, we add a High Dimensional Temporal Signal (HDTS) as in ref. 13. This is an $M$ dimensional periodic signal $\eta[t]$. Given the HDTS period $\tau$, we split the interval $[0, T]$ into $M$ subintervals $I_m, m = 1, \ldots, M$ such that each of the components of $\eta[t]$ is given by $\eta_{I_m}[t] = \left\{\begin{array}{ll} \sin(\eta m t) & \text{if } t \in I_m \\ 0 & \text{otherwise} \end{array}\right.$

This signal is then projected onto the neurons through a decoder $\mu \in \mathbb{R}^{N \times M}$ similar to $\eta$ in Eq. (10). The total current is then given by $r[t] = I_{\mathbf{I}}[t] + I_{\mathbf{r}}[t] + \mu \theta r[t]$.

The aim of FORCE learning is to approximate a $K$-dimensional time-varying teaching signal $\eta[t]$. The vector $\eta[t]$ is used to obtain an approximant of the desired signal $\hat{\eta}[t] = \phi^T \theta r[t]$.

The weights are updated using the RLS learning rule according to:

\[
\phi[t] = \phi[t - 1] - \epsilon t P[t] r[t] 
\]

\[
P[t] = P[t - 1] - \frac{P[t - 1] r[t] \theta^T P[t - 1] r[t]}{1 + r[t]^T P[t - 1] r[t]} 
\]

During the training phase, the teaching signal $\eta[t]$ is used to perform the RLS update. Then, during the testing phase, the teaching signal is removed.

We used the parameters given in Table 4 for all FORCE experiments, unless otherwise specified. For the gamma initialised synaptic time constants, we draw the values from $\mathcal{U}(3, 0.025)$.

The period $\tau$ was chosen to be equal to the length of the teaching signal $\eta[t]$. The membrane potentials were randomly initialised following a uniform distribution, we used the other factors for the experiments (Table 2) but we scaled the standard deviation to be $f$ times that of the original Gamma distribution. We used $f = 4$ for the heterogeneous case.

For the intermediate case, all neurons were initialised as in the Homogeneous configuration except for 5% of them selected randomly that were given the largest time constant value allowed of 100 ms. The aim of this was to test whether all that was needed was some neurons with a longer memory. We chose 5% since the optimal distribution of trained time constants in the SHD shows that about this fraction of neurons reach this maximum value.

In order to improve generalisation, we added noise to the input by adding spikes following a Poisson process with a rate of 1.2 Hz and deleting spikes with a probability of 0.001.

The parameters used for the network are also given in Tables 2 and 3, unless otherwise specified. In Fig. 2F, we used a log-normal distribution for the initial values of the time constants in which we ensured the mode was the same as in the Gamma distribution, we used for the other experiments (Table 2) but we scaled the standard deviation to be $f$ times that of the original Gamma distribution. We used $f = 4$ for the heterogeneous case.

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distribution \( U(U_c, U_{0d}) \). Vectors \( \eta \) and \( \mu \) were randomly drawn from \( U(-1.1) \). The static weights \( v \) were drawn from a normal distribution \( \mathcal{N}(0,1/(Np^3)) \), then these weights were set to 0 with probability \( p = 0.1 \). All other variables are initialised to zero unless otherwise specified.

We computed the errors following

\[
\log \text{MSE}(x, \delta) = \log \left( \frac{||x - \delta||_F^2}{D} \right)
\]

(19)

where \( ||x||_F \) is the Frobenius norm of the multidimensional time signal \( x \) and \( D \) is the number of elements in \( x \).

**Data availability**

**Spiking datasets**

The spiking data used in this study are available in the following databases.

- N-MNIST: https://www.garrickorchard.com/datasets/n-mnist.
- Fashion-MNIST: https://github.com/zalandoresearch/fashion-mnist.
- DVS Gaze: https://www.research.ibm.com/dvgaze.
- Heidelberg Spiking Datasets (HD and SSC): https://compnuro.net/posts/2019-spiking-heidelberg-digits.

**Neural data**

The neural data used in this study are available in the following databases.

- Allen Atlas: https://allennet.readthedocs.io/en/latest.
- Paul Manis dataset: https://figshare.com/articles/dataset/ Raw_voltage_and_current_traces_for_current-voltage_IV_relationships_for_cochlear_neuronales/8854352.

**Audio files**

The Zebra Finch bird song data used in this study is available in the following database.

- Zebra Finch bird song: https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3192758/bin/pone.0025506.002.wav.

**Code availability**

All code is available at https://github.com/npvoid/neural_heterogeneity35.

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**Table 4** FORCE network parameters.

| Parameter | Value | Description |
|-----------|-------|-------------|
| \( \Delta t \) | 0.04 ms | Simulation time step |
| \( N \) | 1000 | Number of neurons |
| \( M \) | 500 | Number of HDTS subintervals |
| \( r_{th} \) | 10 ms | Membrane time constant |
| \( \tau_{th} \) | 20 ms | Synaptic time constant |
| \( U_{th} \) | −40 mV | Membrane threshold |
| \( U_{D} \) | 0 mV | Resting potential |
| \( U_{r} \) | −65 mV | Reset potential |
| \( t_{ref} \) | 2 ms | Refractory time |
| \( Q \) | 10 | Chaotic weight |
| \( G \) | 0.04 | Learned weight |
| \( A \) | 80 | HDTS amplitude |
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Author contributions
These authors contributed equally: N.P.-N. and V.C.H.L. N.P.-N.: conceptualisation, methodology, software, validation, visualisation, writing—original draft; V.C.H.L.: methodology, software, validation, visualisation, writing—review and editing; P.L.D.: writing—review and editing, supervision, project administration; D.F.M.G.: conceptualisation, resources, data curation, writing—review and editing, supervision, project administration.

Competing interests
The authors declare no competing interests.

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