

# PyGeNN: A Python library for GPU-enhanced neural networks

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## 2 ABSTRACT

GPU accelerators are now used in 60% of the Top 10 super computing sites worldwide and are becoming increasingly ubiquitous in workstations and edge computing devices. GeNN is a library written in C++ which generates efficient spiking neural network simulation code to run on GPU devices. However, until now, the full flexibility of GeNN could only be harnessed by writing model descriptions and simulation code in C++. In this paper we present PyGeNN, a Python package which exposes all of GeNN's functionality to Python with minimal overhead. This provides a more user-friendly way of using GeNN and allows modellers to take advantage of the growing Python-based machine learning and computational neuroscience ecosystems. We demonstrate that, in both Python and C++ GeNN simulations, the overheads of recording spiking data can come to dominate simulation times and show how a new spike recording system can reduce these overheads by up to a factor of 10. Using the new recording system, we demonstrate that on a modern GPU, we can use PyGeNN to simulate a full-scale model of a cortical column faster even than real-time neuromorphic systems can achieve. Furthermore, we show that long simulations of a smaller model with complex stimuli and a custom three-factor learning rule defined in PyGeNN can be simulated up to  $72\times$  faster than real-time.

**Keywords:** GPU, high-performance computing, parallel computing, benchmarking, computational neuroscience, spiking neural networks, Python

## 1 INTRODUCTION

A wide range of spiking neural network (SNN) simulators are available, each with their own application domains. NEST (Gewaltig and Diesmann, 2007) is widely used for large-scale point neuron simulations on distributed computing systems; NEURON (Carnevale and Hines, 2006) and Arbor (Akar et al., 2019) specialise in the simulation of complex multi-compartmental models; NeuroKernel (Givon and Lazar, 2016) is focused on emulating fly brain circuits using Graphics Processing Units (GPUs); and CARLsim (Chou et al., 2018), ANNarchy (Vitay et al., 2015), NeuronGPU (Golosio et al., 2020) and GeNN (Yavuz et al., 2016) use GPUs to accelerate point neuron models. For performance reasons, many of these simulators are written in C++ and, especially amongst the older simulators, users describe their models either using a Domain-Specific Language (DSL) or directly in C++. For programming language purists, a DSL may be an elegant way of describing an SNN network model and, for simulator developers, not having to add bindings

to another language is convenient. However, both choices act as a barrier to potential users. Therefore, with both the computational neuroscience and machine learning communities gradually coalescing towards a Python-based ecosystem with a wealth of mature libraries for scientific computing (Hunter, 2007; Van Der Walt et al., 2011; Millman and Aivazis, 2011), exposing spiking neural network simulators to Python seems a pragmatic choice. NEST (Eppler et al., 2009), NEURON (Hines et al., 2009) and CARLsim (Balaji et al., 2020) have all taken this route and now offer a Python interface. Furthermore, newer simulators such as Arbor and Brian2 (Stimberg et al., 2019) have been designed from the ground up with a Python interface.

While we have recently demonstrated some very competitive performance results (Knight and Nowotny, 2018, 2020) using our GeNN simulator (Yavuz2016), it has so far not been usable directly from Python. GeNN can already be used as a backend for the Python-based Brian2 simulator (Stimberg et al., 2019). In brief, the Brian2GeNN interface (Stimberg et al., 2020) modifies the C++ backend “cpp\_standalone” of Brian 2 to generate C++ input files for GeNN. As for cpp\_standalone, initialisation of simulations is mostly done in C++ on the CPU and recording data is saved into binary files and re-imported into Python using Brian 2’s native methods. While Brian2GeNN allows Brian2 users to harness the performance benefits that GeNN provides, it is not possible to expose all of GeNN’s unique features to Python through the Brian2 API. Specifically, GeNN not only allows users to easily define their own neuron and synapse models but, also ‘snippets’ for offloading the potentially costly initialisation of model parameters and connectivity onto the GPU. Additionally, GeNN provides a lot of freedom for users to integrate their own code into the simulation loop. In this paper we describe the implementation of PyGeNN – a Python package which aims to expose the full range of GeNN functionality with minimal performance overheads. While implementing new neuron and synapse models in the majority of other GPU simulators requires extending the underlying C++ code, using PyGeNN, models can be defined directly from Python. Finally, we demonstrate the flexibility and performance of PyGeNN in two scenarios where minimising performance overheads is particularly critical.

- In a simulation of a large, highly-connected model of a cortical microcircuit (Potjans and Diesmann, 2014) with small simulation timesteps. Here the cost of copying spike data off the GPU from a large number of neurons every timestep can become a bottleneck.
- In a simulation of a much smaller model of Pavlovian conditioning (Izhikevich, 2007) where learning occurs over 1 h of biological time and stimuli are delivered – following a complex scheme – throughout the simulation. Here any overheads are multiplied by a large number of timesteps and copying stimuli to the GPU can become a bottleneck.

Using the facilities provided by PyGeNN, we show that both scenarios can be simulated from Python with only minimal overheads over a pure C++ implementation.

## 2 MATERIALS AND METHODS

### 2.1 GeNN

GeNN (Yavuz et al., 2016) is a library for generating CUDA code for the simulation of spiking neural network models. GeNN handles much of the complexity of using CUDA directly as well as automatically performing device-specific optimizations so as to maximize performance.

GeNN consists of a main library – implementing the API used to define models as well as the generic parts of the code generator – and an additional library for each backend (currently there is a reference C++ backend for generating CPU code and a CUDA backend. An OpenCL backend is under development).

70 Users describe their model by implementing a `modelDefinition` function within a C++ file. For example,  
 71 a model consisting of 4 Izhikevich neurons with heterogeneous parameters, driven by a constant input  
 72 current might be defined as follows:

```

73 void modelDefinition(ModelSpec &model)
74 {
75     model.setDT(0.1);
76     model.setName("izhikevich");
77
78     NeuronModels::IzhikevichVariable::VarValues popInit(
79         -65.0, -20.0, uninitialisedVar(), uninitialisedVar(),
80         uninitialisedVar(), uninitialisedVar());
81
82     model.addNeuronPopulation<NeuronModels::IzhikevichVariable>(
83         "Pop", 4, {}, popInit);
84
85     model.addCurrentSource<CurrentSourceModels::DC>(
86         "CS", "Pop", {10.0}, {});
87 }
```

88 The *genn-buildmodel* command line tool is then used to compile this file; link it against the main GeNN  
 89 library and the desired backend library; and finally run the resultant executable to generate the source code  
 90 required to build a simulation dynamic library (a .dll file on Windows or a .so file on Linux and Mac).  
 91 This dynamic library can then either be statically linked against a simulation loop provided by the user or  
 92 dynamically loaded by the user's simulation code. To demonstrate this latter approach, this example uses  
 93 the `SharedLibraryModel` helper class supplied with GeNN to dynamically load the previously defined  
 94 model, initialise the heterogenous neuron parameters and print each neuron's membrane voltage every  
 95 timestep:

```

96 #include "sharedLibraryModel.h"
97
98 int main()
99 {
100     SharedLibraryModel<float> model("./", "izhikevich");
101     model.allocateMem();
102     model.initialize();
103     float *aPop = model.getScalar<float>("a");
104     float *bPop = model.getScalar<float>("b");
105     float *cPop = model.getScalar<float>("c");
106     float *dPop = model.getScalar<float>("d");
107     aPop[0] = 0.02; bPop[0] = 0.2; cPop[0] = -65.0; dPop[0] = 8.0; // RS
108     aPop[1] = 0.1; bPop[1] = 0.2; cPop[1] = -65.0; dPop[1] = 2.0; // FS
109     aPop[2] = 0.02; bPop[2] = 0.2; cPop[2] = -50.0; dPop[2] = 2.0; // CH
110     aPop[3] = 0.02; bPop[3] = 0.2; cPop[3] = -55.0; dPop[3] = 4.0; // IB
111     model.initializeSparse();
112
113     float *vPop = model.getScalar<float>("VPop");
114     while(model.getTime() < 200.0f) {
115         model.stepTime();
116         model.pullVarFromDevice("Pop", "V");

```

```

117         printf("%f, %f, %f, %f, %f\n", t, VPop[0], VPop[1], VPop[2], VPop[3]);
118     }
119     return EXIT_SUCCESS;
120 }

```

## 121 2.2 SWIG

122 In order to use GeNN from Python, both the model creation API and the `SharedLibraryModel`  
 123 functionality need to be ‘wrapped’ so they can be called from Python. While this is possible using  
 124 the API built into Python itself, a wrapper function would need to be manually implemented for each  
 125 GeNN function to be exposed which would result in a lot of maintenance overhead. Instead, we chose  
 126 to use SWIG (Beazley, 1996) to automatically generate wrapper functions and classes. SWIG generates  
 127 Python modules based on special interface files which can directly include C++ code as well as special  
 128 ‘directives’ which control SWIG, for instance:

```

129 %module(package="package") package
130 %include "test.h"

```

131 where the `%module` directive sets the name of the generated module and the package it will be located in  
 132 and the `%include` directive parses and automatically generates wrapper functions for a C++ header file.  
 133 We use SWIG in this manner to wrap both the model building and `SharedLibraryModel` APIs described  
 134 in section 2.1. However, key parts of GeNN’s API such as the `ModelSpec::addNeuronPopulation` method  
 135 employed in section 2.1, rely on C++ templates which are not directly translatable to Python. Instead, valid  
 136 template instantiations need to be given a unique name in Python using the `%template` SWIG directive:

```

137 %template(addNeuronPopulationLIF) ModelSpec::addNeuronPopulation<NeuronModels::LIF>;

```

138 Having to manually add these directives whenever a model is added to GeNN would be exactly the sort of  
 139 maintenance overhead we were trying to avoid by using SWIG. Instead, when building the Python wrapper,  
 140 we search the GeNN header files for the macros used to declare models in C++ and automatically generate  
 141 SWIG `%template` directives.

142 As previously discussed, a key feature of GeNN is the ease with which it allows users to define their  
 143 own neuron and synapse models as well as ‘snippets’ defining how variables and connectivity should be  
 144 initialised. Beneath the syntactic sugar described in our previous work (Knight and Nowotny, 2018), new  
 145 models can be defined in C++ by defining a new class derived from, for example, the `NeuronModels::Base`  
 146 class. The ability to extend this system to Python was a key requirement of PyGeNN and, by using SWIG  
 147 ‘directors’, C++ classes can be made inheritable from Python using a single SWIG directive:

```

148 %feature("director") NeuronModels::Base;

```

## 149 2.3 PyGeNN

150 While GeNN *could* be used from Python via the wrapper generated using the techniques described in the  
 151 previous section, the resultant code would be unpleasant to use directly. For example, rather than being  
 152 able to specify neuron parameters using a native Python data structure such as a list or dictionary, one  
 153 would have to use a wrapped type such as `DoubleVector([0.25, 10.0, 0.0, 0.0, 20.0, 2.0, 0.5])`. To provide  
 154 a more user-friendly and pythonic interface, we have built PyGeNN on top of the wrapper generated by  
 155 SWIG. PyGeNN combines the separate model building and simulation stages of building a GeNN model

in C++ into a single API, likely to be more familiar to users of existing Python-based model description languages such as PyNEST (Eppler et al., 2009) or PyNN (Davison et al., 2008). By combining the two stages together, PyGeNN can provide a unified dictionary-based API for initialising homogeneous and heterogeneous parameters as shown in this re-implementation of the previous example:

```

160 from pygenn import genn_wrapper, genn_model
161
162 model = genn_model.GeNNModel("float", "izhikevich")
163 model.dT = 0.1
164
165 izk_init = {"V": -65.0,
166            "U": -20.0,
167            "a": [0.02, 0.1, 0.02, 0.02],
168            "b": [0.2, 0.2, 0.2, 0.2],
169            "c": [-65.0, -65.0, -50.0, -55.0],
170            "d": [8.0, 2.0, 2.0, 4.0]}
171
172 pop = model.add_neuron_population("Pop", 4, "IzhikevichVariable", {}, izk_init)
173 model.add_current_source("CS", "DC", "Pop", {"amp": 10.0}, {})
174
175 model.build()
176 model.load()
177
178 v = pop.vars["V"].view
179 while model.t < 200.0:
180     model.step_time()
181     model.pull_state_from_device("Pop")
182     print("%t, %f, %f, %f, %f" % (model.t, v[0], v[1], v[2], v[3]))

```

Initialisation of variables with homogeneous values – such as the neurons’ membrane potential – is performed by GeNN and those with heterogeneous values – such as the *a*, *b* and *c* parameters – are initialised by PyGeNN when the model is loaded. While the PyGeNN API is more pythonic and, hopefully, more user-friendly than the C++ interface, it still provides users with the same low-level control over the simulation. Furthermore, by using SWIG’s numpy (Van Der Walt et al., 2011) interface, the host memory allocated by GeNN can be accessed directly from Python using the `pop.vars["V"].view` syntax meaning that no potentially expensive additional copying of data is required.

As illustrated in the previously-defined model, for convenience, PyGeNN allows users to access GeNN’s built-in models. However, one of PyGeNN’s most powerful features is that it enables users to easily define their own neuron and synapse models from within Python. For example, an Izhikevich neuron model (Izhikevich, 2003) can be defined using the `create_custom_neuron_class` helper function which provides some syntactic sugar over the model class inheritance described in the previous section:

```

195 izk_model = genn_model.create_custom_neuron_class(
196     "izk",
197     param_names=["a", "b", "c", "d"],
198     var_name_types=[("V", "scalar"), ("U", "scalar")],
199     sim_code=
200     """
201     $(V)+=0.5*(0.04*$(V)*$(V)+5.0*$(V)+140.0-$(U)+$(Isyn))*DT;

```

```

202     $(V) += 0.5 * (0.04 * $(V) * $(V) + 5.0 * $(V) + 140.0 - $(U) + $(Isyn)) * DT;
203     $(U) += $(a) * ($(b) * $(V) - $(U)) * DT;
204     """ ,
205     threshold_condition_code = "$(V) >= 30.0" ,
206     reset_code =
207         """
208         $(V) = $(c);
209         $(U) += $(d);
210         """ )

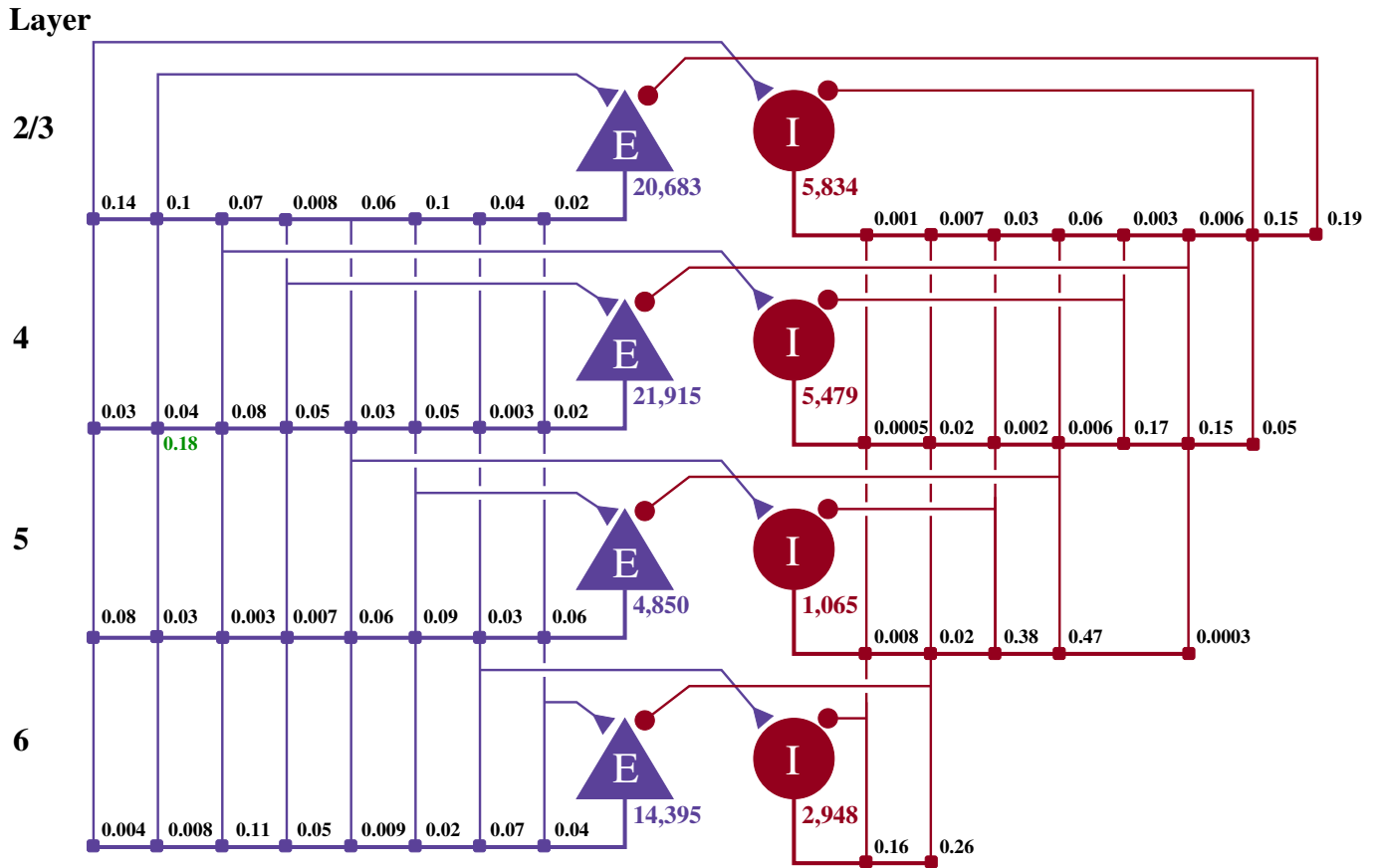
```

211 The `param_names` list defines the real-valued parameters that are constant across the whole population of  
 212 neurons and the `var_name_types` list defines the model state variables and their type (the `scalar` type is  
 213 an alias for single or double-precision floating point, depending on the precision passed to the `GeNNModel`  
 214 constructor). The behaviour of the model can then be defined using a number of code strings. Unlike  
 215 in tools like Brian 2 (Stimberg et al., 2019), these code strings are specified in a C-like language rather  
 216 than in terms of differential equations. This allows expert users to choose their own solver for models  
 217 described in terms of differential equations and to programatically define models such as spike sources.  
 218 For example, in our example model, we chose to implement this neuron using the idiomatic forward Euler  
 219 integration scheme employed by Izhikevich (2003). Finally, the `threshold_condition_code` expression  
 220 defines *when* the neuron will spike whereas the `reset_code` code string defines how the state variables  
 221 should be reset after a spike.

## 222 2.4 Spike recording system

223 Internally, GeNN stores the spikes emitted by a neuron population during one simulation timestep in an  
 224 array containing the indices of the neurons that spiked alongside a counter of how many spikes have been  
 225 emitted. Previously, recording spikes in GeNN was very similar to the recording of voltages shown in the  
 226 previous example code – the array of neuron indices was simply copied from the GPU to the CPU every  
 227 timestep. However, especially when simulating models with a small simulation timestep, such frequent  
 228 synchronization between the CPU and GPU is costly – especially if a higher-level language such as Python  
 229 is involved. Furthermore, biological neurons typically spike at a low rate (in the cortex, the average firing  
 230 rate is only around 3 Hz (Buzsáki and Mizuseki, 2014)) meaning that the amount of spike data transferred  
 231 every timestep is typically very small. To address both of these sources of inefficiency, we have added a  
 232 new data structure to GeNN which stores spike data for many timesteps on device. To reduce the memory  
 233 required for this data structure and to make its size independent of neural activity, the spikes emitted by a  
 234 population of  $N$  neurons in a single simulation timestep are stored in a  $N$ bit bitfield where a ‘1’ represents  
 235 a spike and a ‘0’ the absence of one. Spiking data over multiple timesteps is then represented by bitfields  
 236 stored in a circular buffer. Using this approach, even the spiking output of relatively large models, running  
 237 for many timesteps can be stored in a small amount of memory. For example, the spiking output of a  
 238 model with  $100 \times 10^3$  neurons running for  $10 \times 10^3$  simulation timesteps, required less than 120 MB – a  
 239 small fraction of the memory on a modern GPU. While efficiently handling spikes stored in a bitfield is a  
 240 little trickier than working with a list of neuron indices, GeNN provides an efficient C++ helper function  
 241 for saving the spikes stored in a bitfield to a text file and a numpy-based method for decoding them in  
 242 PyGeNN.





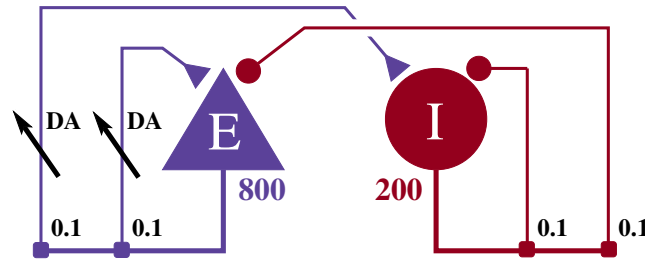
**Figure 1.** Illustration of the microcircuit model. Blue triangles represent excitatory populations, red circles represent inhibitory populations and the numbers beneath each symbol shows the number of neurons in each population. Connection probabilities are shown in small bold numbers at the appropriate point in the connection matrix. All excitatory synaptic weights are normally distributed with a mean of 0.0878 nA (unless otherwise indicated in green) and a standard deviation of 0.008 78 nA. All inhibitory synaptic weights are normally distributed with a mean of 0.3512 nA and a standard deviation of 0.035 12 nA.

## 243 2.5 Cortical microcircuit model

Potjans and Diesmann (2014) developed a cortical microcircuit model of 1 mm<sup>3</sup> of early-sensory cortex. The model consists of 77 169 LIF neurons, divided into separate populations representing the excitatory and inhibitory population in each of 4 cortical layers (2/3, 4, 5 and 6) as illustrated by figure 2. The membrane voltage  $V_i$  of each neuron  $i$  is modelled as

$$\tau_m \frac{dV_i}{dt} = (V_{\text{rest}} - V_i) + R_m (I_{\text{syn}_i} + I_{\text{ext}_i}), \quad (1)$$

where  $\tau_m = 10$  ms and  $R_m = 40$  M $\Omega$  represent the time constant and resistance of the neuron's cell membrane,  $V_{\text{rest}} = -65$  mV defines the resting potential,  $I_{\text{syn}_i}$  represents the synaptic input current and  $I_{\text{ext}_i}$  represents an external input current. When the membrane voltage crosses a threshold  $V_{\text{th}} = -50$  mV a spike is emitted, the membrane voltage is reset to  $V_{\text{rest}}$  and updating of  $V$  is suspended for a refractory period  $\tau_{\text{ref}} = 2$  ms. Neurons in each population are connected randomly with numbers of synapses derived from an extensive review of the anatomical literature. These synapses are current-based, i.e. presynaptic



**Figure 2.** Illustration of the balanced random network model. The blue triangle represents the excitatory population, the red circle represents the inhibitory population, and the numbers beneath each symbol show the number of neurons in each population. Connection probabilities are shown in small bold numbers at the appropriate point in the connection matrix. All excitatory synaptic weights are plastic and initialised to 1 and all inhibitory synaptic weights are initialised to  $-1$ .

spikes lead to exponentially-decaying input currents  $I_{\text{syn}_i}$

$$\tau_{\text{syn}} \frac{dI_{\text{syn}_i}}{dt} = -I_{\text{syn}_i} + \sum_{i=0}^n w_{ij} \sum_{t_j} \delta(t - t_j), \quad (2)$$

where  $\tau_{\text{syn}} = 0.5$  ms represents the synaptic time constant and  $t_j$  are the arrival times of incoming spikes from  $n$  presynaptic neurons. Within each synaptic projection, all synaptic strengths and transmission delays are normally distributed using the parameters presented in Potjans and Diesmann (2014, table 5) and, in total, the model has approximately  $0.3 \times 10^9$  synapses. As well as receiving synaptic input, each neuron in the network also receives an independent Poisson input current, representing input from neighbouring not explicitly modelled cortical regions. The Poisson input is delivered to each neuron via  $I_{\text{ext}_i}$  with

$$\tau_{\text{syn}} \frac{dI_{\text{ext}_i}}{dt} = -I_{\text{ext}_i} + J \text{Poisson}(\nu_{\text{ext}} \Delta t), \quad (3)$$

244 where  $\tau_{\text{syn}} = 0.5$  ms,  $\nu_{\text{ext}}$  represents the mean input rate and  $J$  represents the weight. The ordinary  
 245 differential equations 1, 2 and 3 are solved with an exponential Euler algorithm. For a full description of the  
 246 model parameters, please refer to Potjans and Diesmann (2014, tables 4 and 5) and for a description of the  
 247 strategies used by GeNN to parallelise the initialisation and subsequent simulation of this network, please  
 248 refer to Knight and Nowotny (2018, section 2.3). This model requires simulation using a relatively small  
 249 timestep of 0.1 ms, making the overheads of copying spikes from the GPU every timestep particularly  
 250 problematic.

## 251 2.6 Pavlovian conditioning model

252 The cortical microcircuit model described in the previous section is ideal for exploring the performance  
 253 of short simulations of relatively large models. However, the performance of longer simulations  
 254 of smaller models is equally vital. **(TODO: DETERMINE E.G. PERCENTAGE MODELS E.G. ON**  
 255 **OPENSOURCEBRAIN WHICH ARE SMALL).** Such models can be particularly troublesome for GPU  
 256 simulation as, not only might they not offer enough parallelism to fully occupy the device but, each  
 257 timestep can be simulated so quickly that the overheads of launching kernels etc can dominate. Additional  
 258 overheads can be incurred when models require injecting external stimuli throughout the simulation. Longer  
 259 simulations are particularly useful when exploring synaptic plasticity so, to explore the performance



of PyGeNN in this scenario, we simulate a model of Pavlovian conditioning using a three-factor Spike-Timing-Dependent Plasticity (STDP) learning rule (Izhikevich, 2007).

## 2.6.1 Neuron model

This model consists of an 800 neuron excitatory population and a 200 neuron inhibitory population, within which, each neuron  $i$  is modelled using the Izhikevich model (Izhikevich, 2003) whose dimensionless membrane voltage  $V_i$  and adaption variables  $U_i$  evolve such that:

$$\frac{dV_i}{dt} = 0.04V_i^2 + 5V_i + 140 - U_i + I_{\text{syn}_i} + I_{\text{ext}_i} \quad (4)$$

$$\frac{dU_i}{dt} = a(bV_i - U_i) \quad (5)$$

When the membrane voltage rises above 30, a spike is emitted and  $V_i$  is reset to  $c$  and  $d$  is added to  $U_i$ . Excitatory neurons use the regular-spiking parameters (Izhikevich, 2003) where  $a = 0.02$ ,  $b = 0.2$ ,  $c = -65.0$ ,  $d = 8.0$  and inhibitory neurons use the fast-spiking parameters (Izhikevich, 2003) where  $a = 0.1$ ,  $b = 0.2$ ,  $c = -65.0$ ,  $d = 2.0$ . Again,  $I_{\text{syn}_i}$  represents the synaptic input current and  $I_{\text{ext}_i}$  represents an external input current. While there are numerous ways to solve equations 4 and 5 (Humphries and Gurney, 2007; Hopkins and Furber, 2015; Pauli et al., 2018), we chose to use the forward Euler integration scheme employed by Izhikevich (2003). Under this scheme, equation 4 is first integrated for two 0.5 ms timesteps and then, based on the updated value of  $V_i$ , equation 5 is integrated for a single 1 ms timestep.

## 2.6.2 Synapse models

The excitatory and inhibitory neural populations are connected recurrently, as shown in figure 2, with instantaneous current-based synapses:

$$I_{\text{syn}_i}(t) = \sum_{j=0}^n w_{ij} \sum_{t_j} \delta(t - t_j), \quad (6)$$

where  $t_j$  are the arrival times of incoming spikes from  $n$  presynaptic neurons. Inhibitory synapses are static with  $w_{ij} = -1.0$  and excitatory synapses are plastic. Each plastic synapse has an eligibility trace  $C_{ij}$  as well as a synaptic weight  $w_{ij}$  and these evolve according to a three-factor STDP learning rule (Izhikevich, 2007):

$$\frac{dC_{ij}}{dt} = -\frac{C_{ij}}{\tau_c} + \text{STDP}(\Delta t)\delta(t - t_{\text{pre/post}}) \quad (7)$$

$$\frac{dw_{ij}}{dt} = -C_{ij}D_j \quad (8)$$

where  $\tau_c = 1000$  ms represents the decay time constant of the eligibility trace and  $\text{STDP}(\Delta t)$  describes the magnitude of changes made to the eligibility trace based on the relative timing of a pair of pre and postsynaptic spikes with temporal difference  $\Delta t = t_{\text{post}} - t_{\text{pre}}$ . These changes are only applied to the trace at the times of pre and postsynaptic spikes as indicated by the Dirac delta function  $\delta(t - t_{\text{pre/post}})$ . Here, a

double exponential STDP kernel is employed such that:

$$\text{STDP}(\Delta t) = \begin{cases} A_+ \exp\left(-\frac{\Delta t}{\tau_+}\right) & \text{if } \Delta t > 0 \\ A_- \exp\left(\frac{\Delta t}{\tau_-}\right) & \text{if } \Delta t < 0 \\ 0 & \text{otherwise} \end{cases} \quad (9)$$

where the time constant of the STDP window  $\tau_+ = \tau_- = 20$  ms and the strength of potentiation and depression are  $A_+ = 0.1$  and  $A_- = 0.15$  respectively. Finally, each excitatory neuron has an additional variable  $D_j$  which describes extracellular dopamine concentration:

$$\frac{D_j}{t} = -\frac{D_j}{\tau_d} + \text{DA}(t) \quad (10)$$

272 where  $\tau_d = 200$  ms represents the time constant of dopamine uptake and  $\text{DA}(t)$  the dopamine input over  
273 time.

### 274 2.6.3 PyGeNN implementation of three-factor STDP

275 The first step in implementing this learning rule in PyGeNN is to implement the STDP updates and decay  
276 of  $C_{ij}$ . First, we create a new ‘weight update model’ with the learning rules parameters and the  $w_{ij}$  and  
277  $C_{ij}$  state variables:

```
278 izhikevich_stdp_model = create_custom_weight_update_class(
279     "izhikevich_stdp",
280
281     param_names=["tauPlus", "tauMinus",
282                 "tauC", "aPlus", "aMinus"],
283     var_name_types=[("w", "scalar"), ("c", "scalar")],
```

284 We then instruct GeNN to record the times of current and previous pre and postsynaptic spikes. **(TODO:**  
285 **IMPROVE SENTENCE)** The current spike time will equal the current time if a spike of this sort is being  
286 processed in the current timestep whereas the previous spike time only tracks spikes which have occur  
287 *before* the current timestep:

```
288     is_pre_spike_time_required=True,
289     is_post_spike_time_required=True,
290
291     is_prev_pre_spike_time_required=True,
292     is_prev_post_spike_time_required=True,
```

293 Next we define the ‘sim code’ which is called whenever presynaptic spikes arrive at the synapse. This code  
294 first implements equation 6 – adding the synaptic weight ( $w_{ij}$ ) to the postsynaptic neuron’s input ( $I_{\text{syn}_i}$ )  
295 using the  $\$(\text{addToInSyn}, x)$  function.

```
296     sim_code=
297         """
298         $(addToInSyn, $(w));
```

299 Now we need to calculate the time that has elapsed since the last update of  $C_{ij}$  using the spike times we  
300 previously requested that GeNN record. Within a timestep, GeNN processes presynaptic spikes before

postsynaptic spikes so the time of the last update to  $C_{ij}$  will be the latest time either type of spike was processed in previous timesteps:

```
303         const scalar tc = fmax($(prev_sT_pre),
304                                $(prev_sT_post));
```

Using this time, we can now calculate how much to decay  $C_{ij}$  following equation 7:

```
306         const scalar tagDecay = exp(-$(t) - tc) / $(tauC));
307         scalar newTag = $(c) * tagDecay;
```

To complete the ‘sim code’ we calculate the depression case of equation 9 (here we use the *current* postsynaptic spike time as, if a postsynaptic and presynaptic spike occur in the same timestep, there should be no update).

```
311         const scalar dt = $(t) - $(sT_post);
312         if (dt > 0) {
313             newTag -= ($(aMinus) * exp(-dt / $(tauMinus)));
314         }
315         $(c) = newTag;
316         """,
```

Finally we define the ‘learn post code’ which is called whenever a postsynaptic spike arrives at the synapse. Other than implementing the potentiation case of equation 9 and using the *current* presynaptic spike time when calculating the time since the last update of  $C_{ij}$  – in order to correctly handle presynaptic updates made in the same timestep – this code is very similar to the sim code:

```
321     learn_post_code=
322         """
323         const scalar tc = fmax($(sT_pre),
324                                $(prev_sT_post));
325
326         const scalar tagDecay = exp(-$(t) - tc) / $(tauC));
327         scalar newTag = $(c) * tagDecay;
328
329         const scalar dt = $(t) - $(sT_pre);
330         if (dt > 0) {
331             newTag += ($(aPlus) * exp(-dt / $(tauPlus)));
332         }
333         $(c) = newTag;
334         """)
```

Adding the synaptic weight  $w_{ij}$  update described by equation 8 requires two components. In addition to pre and postsynaptic spikes, the weight update model needs to receive events whenever dopamine is injected via DA. **(TODO: IMPROVE SENTANCE)** GeNN supports such events via the ‘spike-like event’ system which allows events to be triggered based on a condition applied to the presynaptic neuron. In this case, this condition is simply used to check an `injectDopamine` flag set by the dopamine injection logic in our presynaptic neuron model:

```
341     event_threshold_condition_code="injectDopamine",
```

342 In order to extend our event-driven update of  $C_{ij}$  to include these events we need to instruct GeNN to  
 343 record the times at which they occur:

```
344     is_pre_spike_event_time_required=True,
345     is_prev_pre_spike_event_time_required=True,
```

346 The spike-like events can now be handled using an ‘event code’ string:

```
347     event_code=
348         """
349         const scalar tc = fmax($(sT_pre), fmax($(prev_sT_post), $(prev_seT_pre)));
350         const scalar tagDecay = exp(-$(t) - tc) / $(tauC));
351         $(c) *= tagDecay;
352         """,
```

After updating the previously defined calculations of  $t_c$  in the sim code and learn post code to also include the times of spike-like events, all that remains is to update  $w_{ij}$ . Mikaitis et al. (2018) showed how equation 8 could be integrated algebraically, allowing  $w_{ij}$  to be updated in an event-driven manner with:

$$\Delta w_{ij} = \frac{C(t_c^{last})D(t_d^{last})}{-\left(\frac{1}{\tau_c} + \frac{1}{\tau_d}\right)} \left( e^{-\frac{t-t_c^{last}}{\tau_c}} e^{-\frac{t-t_d^{last}}{\tau_d}} - e^{-\frac{t_w^{last}-t_c^{last}}{\tau_c}} e^{-\frac{t_w^{last}-t_d^{last}}{\tau_d}} \right) \quad (11)$$

where  $t_c^{last}$ ,  $t_w^{last}$  and  $t_d^{last}$  represent the last times at which  $C_{ij}$ ,  $W_{ij}$  and  $D_j$  respectively were updated. Because we will always update  $w_{ij}$  and  $C_{ij}$  together when presynaptic, postsynaptic and spike-like events occur,  $t_c^{last} = t_w^{last}$  and equation 12 can be simplified to:

$$\Delta w_{ij} = \frac{C(t_c^{last})D(t_d^{last})}{-\left(\frac{1}{\tau_c} + \frac{1}{\tau_d}\right)} \left( e^{-\frac{t-t_c^{last}}{\tau_c}} e^{-\frac{t-t_d^{last}}{\tau_d}} - e^{-\frac{t_c^{last}-t_d^{last}}{\tau_d}} \right) \quad (12)$$

353 and this update can now be added to each of our three event handling code strings to complete the  
 354 implementation of the learning rule.

#### 355 2.6.4 PyGeNN implementation of Pavlovian conditioning experiment

356 To perform the Pavlovian conditioning experiment using this model, we chose 100 random groups of 50  
 357 neurons (each representing stimuli  $S_1 \dots S_{100}$ ) are chosen from amongst the two neural populations. Stimuli  
 358 are presented to the network in a random order, separated by intervals sampled from  $U(100, 300)$ ms. The  
 359 neurons associated with an active stimulus are stimulated for a single 1 ms simulation timestep with a  
 360 current of 40.0 nA, in addition to the random background current of  $U(-6.5, 6.5)$ nA, delivered to each  
 361 neuron via  $I_{ext_i}$  throughout the simulation.  $S_1$  is arbitrarily chosen as the Conditional Stimuli (CS) and,  
 362 whenever this stimuli is presented, a reward in the form of an increase in dopamine is delivered by setting  
 363  $DA(t) = 0.5$  after a delay sampled from  $U(0, 1000)$ ms. This delay period is large enough to allow a few  
 364 irrelevant stimuli to be presented which act as distractors. The simplest way to implement this stimulation  
 365 regime is to add a current source to the excitatory and inhibitory neuron populations which adds the  
 366 uniformly-distributed input current to an externally-controllable per-neuron current. In PyGeNN, the  
 367 following model can be defined to do just that:

```
368 stim_noise_model = create_custom_current_source_class(
369     "stim_noise",
```

```

370 param_names=["n"],
371 var_name_types=[("iExt", "scalar", VarAccess_READ_ONLY)],
372 injection_code=
373     """
374     $(injectCurrent, $(iExt) + ($(gennrand_uniform) * $(n) * 2.0) - $(n));
375     """

```

where the `n` parameter sets the magnitude of the background noise, the `$(injectCurrent, I)` function injects a current of  $I$  nA into the neuron and `$(gennrand_uniform)` uses the ‘XORWOW’ pseudo-random number generator provided by cuRAND (TODO: CITE) to sample from  $U(0, 1)$ . Once a current source population using this model has been instantiated and a memory view to `iExt` obtained in the manner described in section 2.3, in timesteps when stimulus injection is required, current can be injected into the list of neurons contained in `stimuli_input_set` with:

```

382 curr_ext_view[stimuli_input_set] = 40.0
383 curr_pop.push_var_to_device("iExt")

```

The same approach can then be used to zero the current afterwards. However, as almost 20 000 stimuli will be injected over the course of a 1 h simulation, in order to reduce potential overheads, we can offload the stimulus delivery entirely to the GPU using the following slightly more complex model:

```

387 stim_noise_model = create_custom_current_source_class(
388     "stim_noise",
389     param_names=["n", "stimMagnitude"],
390     var_name_types=[("startStim", "unsigned int"),
391                     ("endStim", "unsigned int", VarAccess_READ_ONLY)],
392     extra_global_params=[("stimTimes", "scalar*")],
393     injection_code=
394         """
395         scalar current = ($(gennrand_uniform) * $(n) * 2.0) - $(n);
396         if($(startStim) != $(endStim) && $(t) >= $(stimTimes)[$(startStim)]) {
397             current += $(stimMagnitude);
398             $(startStim)++;
399         }
400         $(injectCurrent, current);
401         """

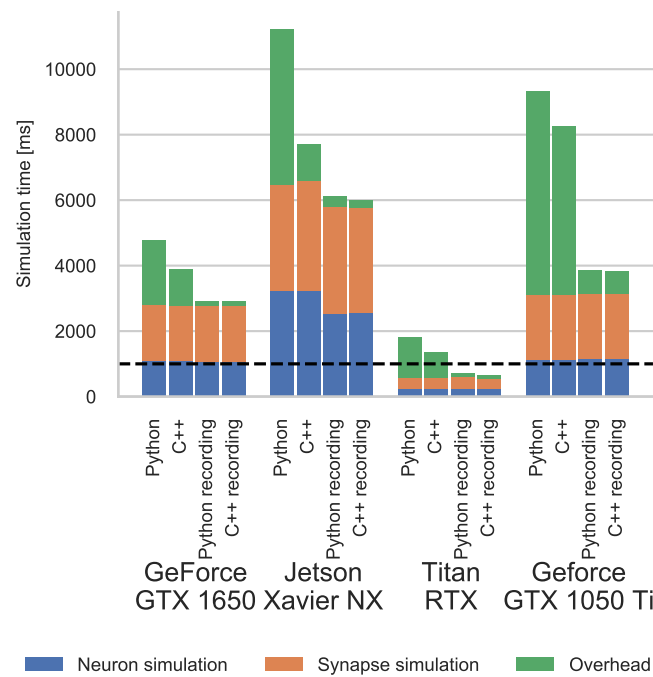
```

This model retains the same logic for generating background noise but, additionally, uses a simple sparse matrix data structure to store the times at which each neuron should have current injected. (TODO: FIGURE) The `startStim` and `endStim` variables point to the subset of the `stimTimes` array used by each neuron’s current source and, once the simulation time `$(t)` passes the time pointed to by `startStim`, current is injected and `startStim` is advanced. This array is stored in a ‘extra global parameter’ which is a read-only memory area that can be allocated and populated from PyGeNN, in this case by ‘stacking’ together a list of lists of spike times:

```

409 curr_pop.set_extra_global_param("stimTimes", np.hstack(neuron_stimuli_times))

```



**Figure 3.** Simulation times of the microcircuit model running on various GPU hardware for 1 s of biological time. ‘Overhead’ refers to time spent in simulation loop but not within CUDA kernels. The dashed horizontal line indicates realtime performance

### 3 RESULTS

In the following subsections we will analyse the performance of the models introduced in sections 2.5 and 2.6 on a representative selection of NVIDIA GPU hardware:

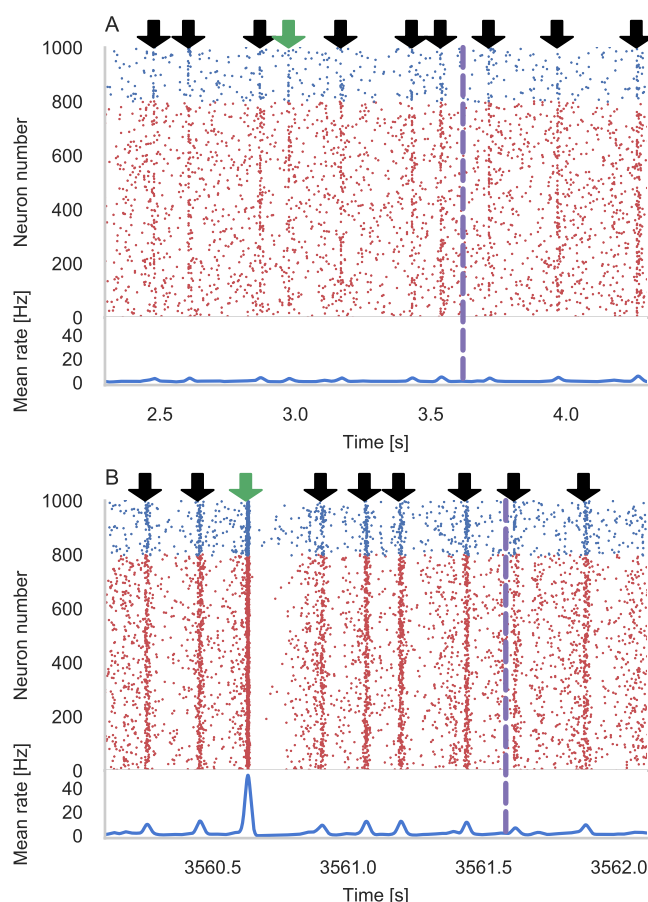
- Jetson Xavier NX – a low-power embedded system with a GPU based on the Volta architecture with 8 GB of shared memory.
- GeForce GTX 1050Ti – a low-end desktop GPU based on the Pascal architecture with 4 GB of dedicated memory.
- GeForce GTX 1650 – a low-end desktop GPU based on the Turing architecture with 4 GB of dedicated memory.
- Titan RTX – a high-end workstation GPU based on the Turing architecture with 24 GB of dedicated memory.

All of these systems run Ubuntu 18 apart from the system with the GeForce 1050 Ti which runs Windows 10.

#### 3.1 Cortical microcircuit model performance

Figure 3 shows the simulation times for the full-scale microcircuit model and, as one might predict, the Jetson Xavier NX is slower than the three desktop GPUs. However, considering that it only consumes a maximum of 15 W compared to 75 W or 320 W for the GeForce cards and Titan RTX respectively, it still performs impressively. The time taken to actually simulate the models (‘Neuron simulation’ and ‘Synapse simulation’) are the same when using Python and C++ as all GeNN optimisation options are exposed to PyGeNN. Interestingly, when simulating *this* model, the larger L1 cache and architectural

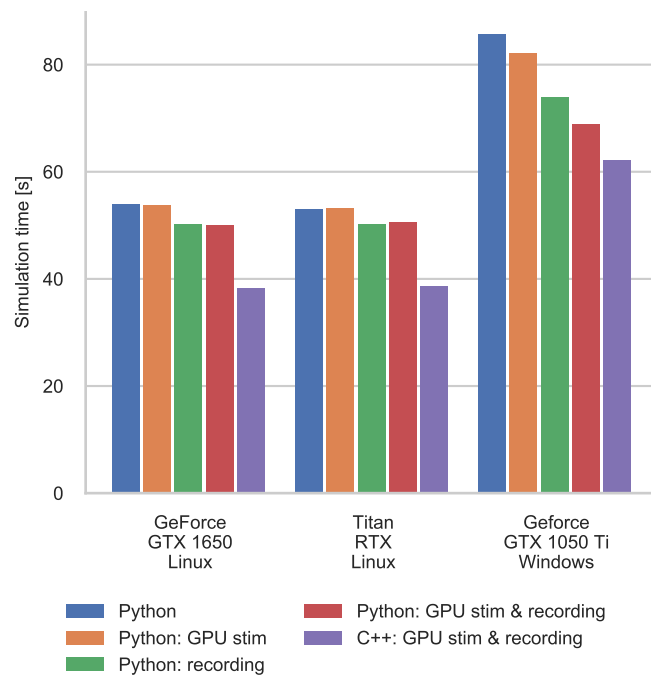




**Figure 4.** Results of Pavlovian conditioning experiment. Raster and spike density plots showing activity centred around first delivery of Conditional Stimulus (CS) during initial (A) and final (B) 50 s of simulation. Downward green arrows indicate times at which CS is delivered and downward black arrows indicate times when other, un-rewarded stimuli are delivered. Vertical dashed lines indicate times at which dopamine is delivered

improvements present in the Turing-based GTX 1650 do not result in significantly improved performance over the Pascal-based GTX 1050Ti. Instead, the slightly improved performance of the GTX 1650 can probably be explained by its additional 128 CUDA cores.

Without the recording system described in section 2.4, the CPU and GPU need to be synchronised after every timestep to allow spike data to be copied off the GPU and stored in a suitable data structure. The ‘overheads’ shown in figure 3 indicate the time taken by these processes as well as the unavoidable overheads of launching CUDA kernels etc. Because Python is an interpreted language, updating the spike data structures is somewhat slower and this is particularly noticeable on devices with a slower CPU such as the Jetson Xavier NX. However, unlike the desktop GPUs, the Jetson Xavier NX’s 8 GB of memory is shared between the GPU and the CPU meaning that data doesn’t have to be copied between their memories and can instead be accessed by both. While, using this shared memory for recording spikes reduces the overhead of copying data off the device, because the GPU and CPU caches are not coherent, caching must be disabled on this memory which reduces the performance of the neuron kernel. Although the Windows machine has a relatively powerful CPU, the overheads measured in both the Python and C++ simulations run on this system are extremely large due to additional queuing between the application and



**Figure 5.** Simulation times of the Pavlovian Conditioning model running on various GPU hardware for 1 h of biological time. (TODO: EXPLANATION OF BARS)

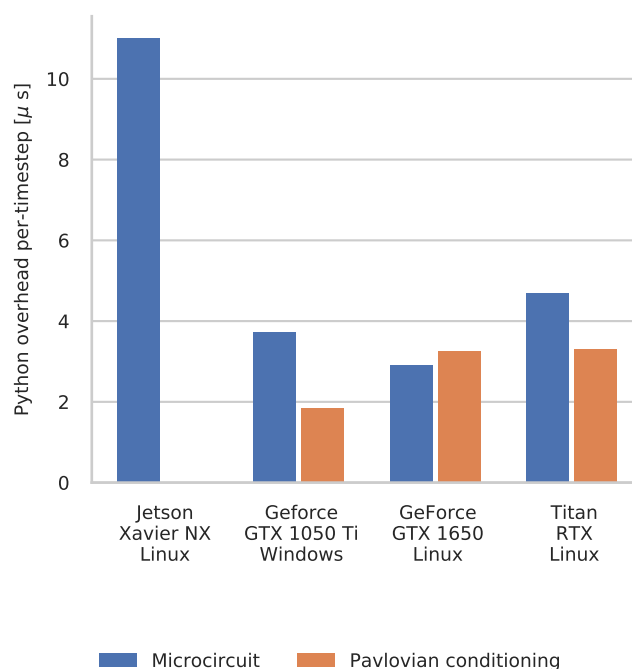
the GPU driver caused by the Windows Display Driver Model (WDDM). When small – in this case 0.1 ms – simulation timesteps are used, this makes per-timestep synchronisation disproportionately expensive.

However, when the spike recording system described in section 2.4 is used, spike data is kept in GPU memory until the end of the simulation and overheads are reduced by up to  $10\times$ . Because synchronisation with the CPU is no longer required every timestep, simulations run approximately twice as fast on the Windows machine. Furthermore, on the high-end desktop GPU, the simulation now runs faster than real-time in both Python and native C++ versions – significantly faster than other recently published GPU simulators (Golosio et al., 2020) and even specialised neuromorphic systems (Rhodes et al., 2020).

### 3.2 Pavlovian conditioning performance

Figure 4 shows the results of an example simulation of the Pavlovian conditioning model. At the beginning of each simulation (Figure 4A), the neurons representing every stimulus respond equally. However, after 1 h of simulation, the response to the CS becomes much stronger (Figure 4B) – showing that these neurons have been selectively associated with the stimulus even in the presence of the distractors and the delayed reward.

In figure 5, we show the runtime performance of simulations of the Pavlovian conditioning model, running on a selection of desktop GPUs using PyGeNN with and without the recording system described in section 2.4 and the optimized stimuli-delivery described in section 2.6. These PyGeNN results are compared to a C++ simulation using both optimizations. Interestingly the Titan RTX and GTX 1650 perform identically in this benchmark with speedups ranging from  $62\times$  to  $72\times$  real-time. This is because, as discussed previously, this model is simply not large enough to fill the 4608 CUDA cores present on the Titan RTX. Therefore, as the two GPUs share the same Turing architecture and have very similar clock speeds (1350 MHz–1770 MHz for the Titan RTX and 1485 MHz–1665 MHz for the GTX 1650), the two GPUs



**Figure 6.** Comparison of per-timestep overhead in microcircuit and Pavlovian conditioning experiments.

perform very similarly. Furthermore, on these two systems, while using the recording system significantly improves performance, the impact of delivering stimuli on the GPU is minimal. However, unlike in the simulations of the microcircuit model, here the GTX 1050 Ti performs rather differently. Although the clock speed of this device is approximately the same as the other GPUs (1290 MHz–1392 MHz) and it has a similar number of CUDA cores to the GTX 1650, its performance is significantly worse. The difference in performance across all configurations is likely to be due to architectural differences between the older Pascal; and newer Volta and Turing architectures. Specifically, Pascal GPUs have one type of Arithmetic Logic Unit (ALU) which handles both integer and floating point arithmetic whereas, the newer Volta and Turing architectures have equal numbers of dedicated integer and floating point ALUs as well as significantly larger L1 caches. As discussed in our previous work (Knight and Nowotny, 2018), these architectural features are particularly beneficial for SNN simulations with STDP where a large amount of floating point computation is required to update the synaptic state *and* additional integer arithmetic is required to calculate the indices into the sparse matrix data structures. Furthermore, due to the additional synchronisation overheads caused by the Windows Display Driver Model (WDDM) which we discussed in the previous section, offloading stimuli delivery to the GPU improves the performance significantly on the Windows machine.

The difference between the speeds of the Python and C++ simulations of the Pavlovian conditioning model (figure 5) *appear* much larger than those of the microcircuit model (figure 3). However, as figure 6 illustrates, the difference between the duration of individual timestep in Python and C++ simulations of both models is approximately constant and consistent with the cost of a small number of Python to C++ function calls (Apache Crail, 2019). However, depending on the size and complexity of the model as well as the hardware used, this overhead may still be significant. **(TODO: NOT REALLY SURE WHETHER SIGNIFICANT IS WHAT WE WANT TO SAY HERE)** For example, when simulating the microcircuit model

for 1 s on the Titan RTX, the overhead of using Python is less than 0.2 % but, when simulating the Pavlovian conditioning model on the same device, the overhead of using Python is almost 31 %.

## 4 DISCUSSION

In this paper we have introduced PyGeNN, a Python interface to the C++ based GeNN library for GPU accelerated spiking neural network simulations.

Uniquely, the new interface provides access to all the features of GeNN, without leaving the comparative simplicity of Python and with, as we have shown, typically negligible overheads from the Python bindings. PyGeNN also allows bespoke neuron and synapse models to be defined from within Python, making PyGeNN much more flexible and broadly applicable than, for instance, the Python interface to NEST (Eppler et al., 2009) or the PyNN model description language used to expose CARLsim to Python (Balaji et al., 2020).

In many ways, the new interface resembles elements of the Python-based Brian 2 simulator (Stimberg et al., 2019) (and it's Brian2GeNN backend (Stimberg et al., 2020)) with two key differences. Unlike in Brian 2, bespoke models in PyGeNN are defined with 'C-like' code snippets. This has the advantage of unparalleled flexibility for the expert user but, comes at the cost of more complexity as the code for a timestep update needs to include a suitable solver as well as merely differential equations. The second difference lies in how data structures are handled. Whereas simulations run using the C++ or Brian2GeNN Brian 2 backends use files to exchange data with Python, the underlying GeNN data structures are directly accessible from PyGeNN meaning that no disk access is involved.

As we have demonstrated, the PyGeNN wrapper, exactly like native GeNN, can be used on a variety of hardware from data centre scale down to mobile devices such as the NVIDIA Jetson. This allows for the same codes to be used in large-scale brain simulations and embedded and embodied spiking neural network research. Supporting the popular Python language in this interface makes this ecosystem available to a wider audience of researchers in both Computational Neuroscience, bio-mimetic machine learning and autonomous robotics.

The new interface also opens up opportunities to support researchers that work with other Python based systems. In the Computational Neuroscience and Neuromorphic computing communities, we can now build a PyNN (Davison et al., 2008) interface on top of PyGeNN and, infact, a prototype of such an interface is in development. Furthermore, for the burgeoning spike-based machine learning community, we can use PyGeNN as the basis for a spike-based machine learning framework akin to TensorFlow or PyTorch for rate-based models. A prototype interface of this sort called mlGeNN is in development and close to release.

Finally, in this work we have introduced a new spike recording system for GeNN and have shown that, using this system, we can now simulate the Potjans microcircuit (Potjans and Diesmann, 2014) model faster than real-time, which thus far was only possible on the large SpiNNaker neuromorphic supercomputer (Rhodes et al., 2020).

- do we need to discuss the wide variety of uses, i.e. MC versus Pavlovian demonstrated in this paper?
- Turing architecture is great for GeNN! Presented results improve on state-of-the-art.
- PyGeNN as an intermediate layer - PyNN, ML
- Cost of C++ - Python calls in models
- something about neuromorphic systems often being real-time / BS accelerated time

## CONFLICT OF INTEREST STATEMENT

528 The authors declare that the research was conducted in the absence of any commercial or financial  
529 relationships that could be construed as a potential conflict of interest.

## AUTHOR CONTRIBUTIONS

530 JK and TN wrote the paper. TN is the original developer of GeNN. AK was the original developer of  
531 PyGeNN. JK is currently the primary developer of both GeNN and PyGeNN and was responsible for  
532 implementing the spike recording system. JK performed the experiments and the analysis of the results that  
533 are presented in this work.

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## DATA AVAILABILITY STATEMENT

537 The datasets [GENERATED/ANALYZED] for this study can be found in the [NAME OF REPOSITORY]  
538 [LINK].

## REFERENCES

- 539 Akar, N. A., Cumming, B., Karakasis, V., Kusters, A., Klijn, W., Peyser, A., et al. (2019). Arbor — A  
540 Morphologically-Detailed Neural Network Simulation Library for Contemporary High-Performance  
541 Computing Architectures. In *2019 27th Euromicro International Conference on Parallel, Distributed  
542 and Network-Based Processing (PDP)* (IEEE), 274–282. doi:10.1109/EMPDP.2019.8671560  
543 [Dataset] Apache Crail (2019). Crail Python API: Python -> C/C++ call overhead  
544 Balaji, A., Adiraju, P., Kashyap, H. J., Das, A., Krichmar, J. L., Dutt, N. D., et al. (2020). PyCARL: A  
545 PyNN Interface for Hardware-Software Co-Simulation of Spiking Neural Network  
546 Beazley, D. M. (1996). Using SWIG to control, prototype, and debug C programs with Python. In *Proc.  
547 4th Int. Python Conf*  
548 Buzsáki, G. and Mizuseki, K. (2014). The log-dynamic brain: how skewed distributions affect network  
549 operations. *Nature reviews. Neuroscience* 15, 264–78. doi:10.1038/nrn3687  
550 Carnevale, N. T. and Hines, M. L. (2006). *The NEURON book* (Cambridge University Press)  
551 Chou, T.-s., Kashyap, H. J., Xing, J., Listopad, S., Rounds, E. L., Beyeler, M., et al. (2018). CARLsim 4:  
552 An Open Source Library for Large Scale, Biologically Detailed Spiking Neural Network Simulation  
553 using Heterogeneous Clusters. In *2018 International Joint Conference on Neural Networks (IJCNN)*  
554 (IEEE), 1–8. doi:10.1109/IJCNN.2018.8489326  
555 Davison, A. P., Brüderle, D., Eppler, J., Kremkow, J., Müller, E., Pecevski, D., et al. (2008). PyNN: A  
556 Common Interface for Neuronal Network Simulators. *Frontiers in neuroinformatics* 2, 11. doi:10.3389/  
557 neuro.11.011.2008



- 558 Eppler, J. M., Helias, M., Muller, E., Diesmann, M., and Gewaltig, M. O. (2009). PyNEST: A convenient  
559 interface to the NEST simulator. *Frontiers in Neuroinformatics* 2, 1–12. doi:10.3389/neuro.11.012.2008
- 560 Gewaltig, M.-O. and Diesmann, M. (2007). NEST (NEural Simulation Tool). *Scholarpedia* 2, 1430
- 561 Givon, L. E. and Lazar, A. A. (2016). Neurokernel: An open source platform for emulating the fruit fly  
562 brain. *PLOS ONE* 11, 1–25. doi:10.1371/journal.pone.0146581
- 563 Golosio, B., Tiddia, G., De Luca, C., Pastorelli, E., Simula, F., and Paolucci, P. S. (2020). A new GPU  
564 library for fast simulation of large-scale networks of spiking neurons , 1–27
- 565 Hines, M. L., Davison, A. P., and Muller, E. (2009). NEURON and Python. *Frontiers in Neuroinformatics*  
566 3, 1–12. doi:10.3389/neuro.11.001.2009
- 567 Hopkins, M. and Furber, S. B. (2015). Accuracy and Efficiency in Fixed-Point Neural ODE Solvers.  
568 *Neural computation* 27, 2148–2182
- 569 Humphries, M. D. and Gurney, K. (2007). Solution Methods for a New Class of Simple Model Neurons M.  
570 *Neural Computation* 19, 3216–3225. doi:doi:10.1162/neco.2007.19.12.3216
- 571 Hunter, J. D. (2007). Matplotlib: A 2D graphics environment. *Computing in Science & Engineering* 9,  
572 90–95. doi:10.1109/MCSE.2007.55
- 573 Izhikevich, E. M. (2003). Simple model of spiking neurons. *IEEE Transactions on neural networks* 14,  
574 1569–72. doi:10.1109/TNN.2003.820440
- 575 Izhikevich, E. M. (2007). Solving the Distal Reward Problem through Linkage of STDP and Dopamine  
576 Signaling. *Cerebral Cortex* 17, 2443–2452. doi:10.1093/cercor/bhl152
- 577 Knight, J. C. and Nowotny, T. (2018). GPUs Outperform Current HPC and Neuromorphic Solutions  
578 in Terms of Speed and Energy When Simulating a Highly-Connected Cortical Model. *Frontiers in*  
579 *Neuroscience* 12, 1–19. doi:10.3389/fnins.2018.00941
- 580 Knight, J. C. and Nowotny, T. (2020). Larger GPU-accelerated brain simulations with procedural  
581 connectivity. *bioRxiv* doi:10.1101/2020.04.27.063693
- 582 Mikaitis, M., Pineda García, G., Knight, J. C., and Furber, S. B. (2018). Neuromodulated Synaptic  
583 Plasticity on the SpiNNaker Neuromorphic System 12, 1–13. doi:10.3389/fnins.2018.00105
- 584 Millman, K. J. and Aivazis, M. (2011). Python for scientists and engineers. *Computing in Science and*  
585 *Engineering* 13, 9–12. doi:10.1109/MCSE.2011.36
- 586 Pauli, R., Weidel, P., Kunkel, S., and Morrison, A. (2018). Reproducing Polychronization: A Guide to  
587 Maximizing the Reproducibility of Spiking Network Models. *Frontiers in Neuroinformatics* 12, 1–21.  
588 doi:10.3389/fninf.2018.00046
- 589 Potjans, T. C. and Diesmann, M. (2014). The Cell-Type Specific Cortical Microcircuit: Relating Structure  
590 and Activity in a Full-Scale Spiking Network Model. *Cerebral Cortex* 24, 785–806. doi:10.1093/cercor/  
591 bhs358
- 592 Rhodes, O., Peres, L., Rowley, A. G. D., Gait, A., Plana, L. A., Brenninkmeijer, C., et al. (2020). Real-time  
593 cortical simulation on neuromorphic hardware. *Philosophical Transactions of the Royal Society A:*  
594 *Mathematical, Physical and Engineering Sciences* 378, 20190160. doi:10.1098/rsta.2019.0160
- 595 Stimberg, M., Brette, R., and Goodman, D. F. (2019). Brian 2, an intuitive and efficient neural simulator.  
596 *eLife* 8, 1–41. doi:10.7554/eLife.47314
- 597 Stimberg, M., Goodman, D. F., and Nowotny, T. (2020). Brian2GeNN: accelerating spiking neural network  
598 simulations with graphics hardware. *Scientific Reports* 10, 1–12. doi:10.1038/s41598-019-54957-7
- 599 Van Der Walt, S., Colbert, S. C., and Varoquaux, G. (2011). The NumPy array: A structure for efficient  
600 numerical computation. *Computing in Science and Engineering* 13, 22–30. doi:10.1109/MCSE.2011.37
- 601 Vitay, J., Dinkelbach, H., and Hamker, F. (2015). ANNarchy: a code generation approach to neural  
602 simulations on parallel hardware. *Frontiers in Neuroinformatics* 9, 19. doi:10.3389/fninf.2015.00019



- 603 Yavuz, E., Turner, J., and Nowotny, T. (2016). GeNN: a code generation framework for accelerated brain  
604 simulations. *Scientific reports* 6, 18854. doi:10.1038/srep18854