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The use and abuse of large-scale brain models

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We provide an overview and comparison of several recent large-scale brain models. In addition to discussing challenges involved with building large neural models, we identify several expected benefits of pursuing such a research program. We argue that these benefits are only likely to be realized if two basic guidelines are made central to the pursuit. The first is that such models need to be intimately tied to behavior. The second is that models, and more importantly their underlying methods, should provide mechanisms for varying the level of simulated detail. Consequently, we express concerns with models that insist on a 'correct' amount of detail while expecting interesting behavior to simply *emerge*.

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Introduction

One central goal of neuroscience is to understand how complex processes in the brain give rise to complex behavior. Only recently has our understanding of the processes at work in the brain, and our ability to simulate complex processes in general, progressed to the point that this goal seems realistic. Advances in hardware have made the simulation of millions or even billions of neurons possible. Resources aimed at whole brain data collection have provided unprecedented views of brain anatomy and function that can help us to construct and verify large-scale models [1–3]. The quality of such data sets is only likely to improve with the progress of billion dollar projects such as the recently announced Brain Activity Map project (aka the Brain Research through Advancing Innovative Neurotechnologies (BRAIN) initiative) [4], which intends to develop experimental methods for recording unprecedented numbers of neurons in an active neural circuit.

As such resources become available, it is critical to ask: How can we best make use of these resources to succinctly quantify our understanding of brain function? We believe that, given the analytic intractability of a system as complex and nonlinear as the brain, large-scale modeling will play a crucial role. That is, we must build a brain to know one. As Richard Feynman famously noted: ''That which I cannot create, I do not understand'' [5].

However, there are a wide variety of ways we might proceed in creating a simulated brain. Consequently, we review several past large-scale models to characterize different approaches (see also [6,7] for reviews), describe the benefits we might expect of such models, and ultimately discuss what lessons can be drawn regarding the continued development of ever larger and more sophisticated brain models. To be specific, we are focussing on large-scale brain models that span multiple brain areas and whose output is the product of large numbers of simulated neurons (e.g. over a million). These large-scale brain models are a subclass of large-scale neural simulations.

Notable large-scale brain models

Izhikevich and Edelman

One of the first brain-scale models ever developed was the 100 million neuron thalamocortical model developed by Izhikevich and Edelman [8]. It included 22 different types of multi-compartmental neurons in cortex and thalamus, wired together by about 500 million synapses, which captured synaptic dynamics including short-term plasticity and STDP. The model exhibited phenomena that are known to exist in the human brain, such as spontaneous activity and rhythms of spiking activity.

The Human Brain Project

One of the most highly publicized large-scale brain models is the Blue Brain Project, started in 2005 [9]. The Human Brain Project (HBP) [10••], which was recently approved for one billion euros of funding from the European Union, has the Blue Brain model as its centerpiece. The stated goal of the HBP is to build a working simulation of the entire human brain. The model is focused on simulating cortical columns, hypothesized cylindrical groups of approximately 100,000 neurons that make up the cerebral cortex of mammals [11,12], but see also [13]. The largest simulations of this model to date have included about a million neurons. Each neuron and synapse is simulated in a great deal of detail, taking into account ion channel composition, spatial morphology and detailed physiological data [14]. The majority of data used in the model is gathered from rodent slice experiments and connectivity is determined by the statistical properties of observed connectivity across slices [15]. The project is expected to allow ''tracking the emergence of intelligence'' [9].

The DARPA Synapse Project

Another large-scale model currently under development is part of the DARPA Synapse project [16]. This project was started in 2008, and the cortical model included in this project is based upon previous work simulating hundreds of millions of cortical neurons [17]. In contrast to the HBP, the Synapse project uses a simpler neuron model that includes neural spikes and spike-time-dependent plasticity (STDP), but little in the way of spatial morphology or ionic dynamics. As a result, many more individual neurons can be simulated simultaneously. They have recently reported a model with 500 billion neurons (5 times more than are in the human brain) [18••].

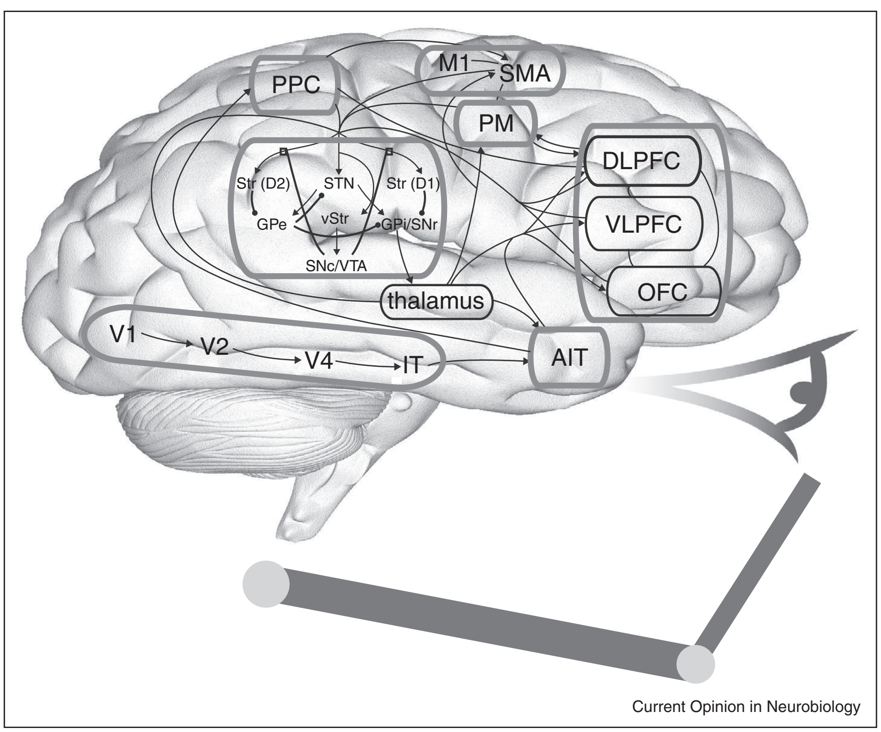
Spaun

Spaun [19••] is a large-scale brain model developed in our lab in 2012. In terms of the single neuron model employed, Spaun is similar to Synapse; it uses a simplified spiking model. In terms of number of cells, it is similar in scale to the HBP, as it uses 2.5 million neurons. The method used to design and construct the model combines the Neural Engineering Framework [20, NEF] and the Semantic Pointer Architecture [21•, SPA]. The NEF provides a quantitative, general approach for implementing high-dimensional nonlinear dynamical systems in networks of spiking neurons. It acts as a 'neural compiler' allowing high-level functional specifications to be mapped to connection weights in low-level spiking neural networks. The SPA provides a particular functional specification that captures central aspects of cortical and subcortical organization and behavior. The SPA defines a neurally plausible representational format (i.e. semantic pointers) that captures perceptual, motor, and cognitive representations. Spaun itself is a specific model that adheres to the SPA and was generated using the NEF. The model includes several cortical and subcortical structures, receiving input in the form of images through a single eye, and generating output by moving its single, physically modeled, arm (see Figure 1). Spaun is able to perform eight different perceptual, motor, and cognitive tasks in any order, without any changes to the model between tasks.

A comparison

The different choices regarding how to construct a large-scale model reflected in these examples has resulted in some friction. Henry Markram has criticized Modha's cat-scale neural model, calling it ''trivial'' and stating: ''It is

Figure 1



A high-level overview of the parts of the brain included in the Spaun model. Each brain area helps extend the functionality of Spaun, though none is specific to a single task. The implementation of a particular function by each area is well-supported by a variety of functional imaging and/or cellular data (see [19••]). The many subsystems are coordinated by a combination of their default connectivity and the flexible effective connectivity controlled by the basal ganglia (figure adapted from [19••] with permission).

Table 1

A comparison of large-scale brain models

Model	Neurons	Synapses	Neuron complexity	Hardware	Behaviors
Izhikevich	1.0×10^8	5.0×10^8	Moderate	Beowolf Cluster (60 3 GHz processors)	Neural level phenomena
HBP	1.0×10^6	5.0×10^8	High	IBM Blue Gene	Neural level phenomena
Synapse	5.0×10^{11}	1.0×10^{14}	Low	IBM Blue Gene	Neural level phenomena
Spaun	2.5×10^6	1.0×10^{12}	Low	8 Core Xeon processor (2.53 GHz)	Simple perceptual, motor, and cognitive tasks

highly unethical of Mohda to mislead the public in making people believe they have actually simulated a cat's brain'' [22•]. As well, Markram commented of the Spaun model: ''It is not a brain model'' [23].

In both cases, Markram is taking issue with what he sees as a lack of biological realism. Such disagreements about how to construct large-scale neural models are important. If we build a model that does not capture relevant aspects of the system, it will not be explanatory or predictive, and hence not useful. What kind of explanations and predictions do the current generation of models provide?

All of the discussed models are concerned to some extent with simulating complex neural activity and replicating neural phenomena found in the brain (see Table 1). They have all replicated some standard measurable properties of the brain including spike patterns, activity waves, and rhythms. However, only the Spaun model connects its complex neural activity to complex behavior. If, indeed, the purpose of neuroscience is to make such a connection, then the ability of a model to explain and predict behavior must be part of determining what is and what is not a good brain model. But, is making such a connection really the purpose of such models? And, if so, what does that mean for the role of biological realism?

Why build large-scale brain models?

Many reasons have been offered as to why large-scale models are important to build. These include the ability to understand mysterious brain disorders, from autism to addiction [24], to develop and test new kinds of medical interventions, be they drugs or stimulation [25], and to provide a way to organize and unify the massive amounts of data generated by the neurosciences [26]. As well, there are studies that are impractical or immoral to perform on living subjects over the long-term [27]. Using brain models can allow us to study neural development without these constraints.

Beyond such practical and ethical considerations, there are basic research questions that can be addressed in new ways in large-scale models. Questions such as: What is the role of neural spiking? If we can construct a large-scale model and demonstrate little to no change in behavior when using non-spiking neurons, suggestions that spikes are for long-distance communication alone [28] will seem more reasonable. If the model fails to function, we would be in an excellent position to understand why. Similar approaches can be taken to other questions, including: ''What kinds of learning can take place without adversely affecting the stability of the whole brain?'' ''What kinds of oscillatory patterns are intrinsic, and which are generated by large cortical network interactions?'' ''Which simplified neuron model best approximates the behavior of a real neuron [29]?'' ''What is the role of heterogeneity in populations of functionally related neurons [30]?''

However, no question seems to loom larger in the minds of modelers than: ''How do brains control behavior?'' Interestingly, all of the lead researchers of the models described earlier have cited a central desire to understand intelligent behavior [9,31,8]. In essence there is agreement that the vast majority of observed behavior is the result of the interactions between many brain areas. Without constructing models that explore these complex interactions, we are unlikely to be able to understand how to help a distressed brain, or explain the basic processes behind biological cognition.

In short, without large-scale models, we cannot test large-scale hypotheses. Without large-scale hypotheses, we cannot address what makes us humans – as the pinnacle of sophisticated behavior – interesting.

But is there a right way to build such models? Is there a right 'level of detail'? We believe that this is simply an ill-posed question. As has long been accepted by those constructing large-scale climate models, the appropriate scale is determined by balancing two things [32]: first, the questions that need to be answered and second, the available computational resources.

If we are asking questions about how changing the morphology of neurons relates to changes in its activity (perhaps to understand the effects of neurofibrillary tangles in Alzheimer's disease), our model likely needs to include neuron morphology. However, if we are asking questions about how neuronal death in hippocampus results in memory loss, perhaps our model can simplify away detailed morphology. The benefit of such simplifications is that we can simulate more neurons using the same computational resources. Just as with models of the weather, larger scale models require more simplifications

Table 2

Example pros and cons to adopting either a top-down or bottom-up approach to brain modeling

	Top-down	Bottom-up
Pros	• Explicitly test high-level hypotheses • Independence from extensive knowledge of missing biological details • Can import expert knowledge from behavioral sciences	• Clear relation of model to measurable detail • Models are more driven by (biological) data • Allowable constraints are more domain specific
Cons	• Hypotheses can bias proposed models • Must make assumptions that go beyond available data • May not contact relevant biological detail	• Reliance on 'emergence' for high-level effects • Must collect missing data • Difficult to relate models to other behavioral sciences

because of computational constraints. And, critically, computational constraints will never be removed, as there are always more details that could be simulated.

Bottom-up modeling versus top-down modeling

There are two broad kinds of approaches to building neural models. The 'bottom-up' approach exemplified by the HBP, entails attempting to simulate the biological processes in the brain in as much detail as possible allowing one ''to study the steps involved in the emergence of biological intelligence'' [9]. In contrast, there is also the 'top-down' approach employed by Spaun and other models [33•,34], which entails identifying hypotheses regarding the behavioral function of a brain area and then determining how neurons carry out the relevant computations with networks of spiking neurons (see Table 2).

The 'top-down' approach allows us to use the vast knowledge gained through the behavioral sciences to impose constraints on the model. This allows us to use the model to test hypotheses about the functions of different brain regions. For example, Spaun implements a specific circuit that models the ability of the basal ganglia to perform action selection [35]. This network has been tested against a wide variety of low-level data (e.g. spike patterns during learning, spike variability, etc.), while exhibiting useful high-level effects (e.g. selecting an action from many alternatives). Spaun further demonstrates that such a model can be used effectively in a large-scale setting. Of course, there is always the concern that such a top-down model has embedded implausible assumptions into the model. However, as with any scientific endeavor, successful comparison of the model to a wide variety of data increases our confidence that the embedded principles parallel those discovered by evolution.

The complementary concern with the bottom-up approach is its reliance on the often mysterious notion of ''emergence'' [36] to produce behavior. It is overly optimistic, if not naive, to assume that simulating neurons in statistically similar-looking patterns to average data will allow interesting behavior to emerge, without explicitly defining a computation for these neurons to perform [37]. If the brain is able to perform complex, high-dimensional computations as presumed by many theorists [38•], explicitly postulating those computations will significantly shorten the road to discovery.

To build on Marr's [39] analogy, consider the task of building an organism capable of flight. A bottom-up approach might reduce a bird to minimal component parts: vanes, barbs, barbules, hackles, or perhaps molecular components. Unfortunately, at low levels a kiwi is very similar to a duck. Perhaps more to the point, the details of feathers are not relevant for understanding flight. The top-down approach, in contrast, would attempt to mimic selected structures thought relevant for flying: perhaps simplified wings, or simplified feathers. The result would be an earlier understanding of the principles of flight, and allow subsequent characterization of the role feathers (and vanes, barbs, etc.). For the brain, we do not know the right level of detail beforehand, but exploring plausible levels *in the context of behavior* is likely to lead, most efficiently, to a good understanding of the structure/function relation.

With these considerations in mind, it seems clear that arguing over the 'right' level of detail for brain models is misguided. We should always ask ''right for what purpose?'' The correct answer will often be controversial. But, building detailed models and simplifying them carefully is a good method for determining the best answers to such questions. Although we use Spaun as an example of top-down modeling here, the methods used to construct it allow us to vary the amount of detail in any part of the model systematically. Providing models and methods that allow for this kind of systematic variation in detail is critical for efficiently constructing large models – and hence critical for exploring the biological *and* behavioral roots of brain function.

Conclusions

In sum, we have identified two critical considerations to guide the effective construction of large-scale models. The first is that a clear link to behavioral constraints must be established. Without such a link, we are missing the fundamental purpose of neuroscience: to understand the relation between brains and behavior. The second consideration is that the level of detail included in a model should be determined by careful trade-offs between that amount of detail, computational resources, and the questions that need to be answered. The most efficient methods for building models will provide a natural means for systematically exploring exactly those tradeoffs.

Beyond such methodological considerations, there are also many practical constraints on building large models. These include the software engineering challenges involved in developing, distributing, and maintaining a codebase for large models. As well, organizing, analyzing, and storing the massive amounts of data that can be generated by large simulations poses familiar, but complex, IT challenges. Having to build and maintain the hardware infrastructure required can also impose a significant strain on finances and time. Critically, several initiatives are helping to provide free, open source resources for the community that help to minimize these burdens even for large-scale models [40–42]. Our group has also developed such software resources, ones that are specifically designed to meet the methodological considerations discussed here (http://nengo.ca/). And, we are working closely with hardware groups to develop specialized large-scale neural modeling infrastructure that uses this same software [43,44]. We believe that the rapid confluence of software, hardware, and theoretical insight aimed at building neural models at previously unheard of scales will usher in a fundamental shift in our understanding of how brains so successfully inhabit their strikingly complex world.

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