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Data-driven models in human neuroscience and neuroengineering

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Discoveries in modern human neuroscience are increasingly driven by quantitative understanding of complex data. Data-intensive approaches to modeling have promise to dramatically advance our understanding of the brain and critically enable neuroengineering capabilities. In this review, we provide an accessible primer to modern modeling approaches and highlight recent data-driven discoveries in the domains of neuroimaging, single-neuron and neuronal population responses, and device neuroengineering. Further, we suggest that meaningful progress requires the community to tackle open challenges in the realms of model interpretability and generalizability, training pipelines of data-fluent human neuroscientists, and integrated consideration of data ethics.

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Introduction

With advances in recording hardware, computing infrastructure, and data storage, human neuroscience has access to a deluge of data from a variety of measurement modalities, including electrophysiology, functional imaging, and behavioral monitoring. These data are likely to escalate in quantity and quality in the foreseeable future, presenting both a tremendous challenge and unprecedented opportunity for insights into the functions and dysfunctions of the human brain. Further, development of data-driven models has the potential to transform neuroengineering applications, including brain-computer interfaces (BCIs) and neuroprostheses to rehabilitate, assist, and augment the human nervous system.

Modeling the human brain is particularly challenging in large part because the data have non-stationary and multi-scale dynamics, exhibit spatial heterogeneity, and are typified by substantial individual variability. Unlike progress toward understanding the neuroscience of non-human model organisms, many observations of human neural computations may be relatively limited in scope, constrained by opportunistic data from clinical sources, and lack true reproducible controls. Many successes in the history of neuroscience have hinged on the availability of accurate biophysical models; however, we are increasingly interested in characterizing systems for which no physical model can be easily written.

Fortunately, innovations in computational approaches are making tractable the analysis, modeling, and prediction of large, multimodal, and unstructured data. The most relevant tools have come from methodlogical domains including data science, statistics, machine learning, dynamical systems, and control theory. Moreover, models can now leverage multiple modalities of measurements, integrating different resolutions and types of data. Large, high-quality datasets are also becoming openly available. Although critical infrastructure is still being developed, there is mounting interest and pressure from the community for data sharing and building open access data repositories (e.g. [1,2]). In the framework of Jim Gray [3], human neuroscience has entered the *fourth paradigm* of data-intensive science, where discoveries are defined by our ability to manage, explore, and disseminate data.

In this review, we define data-driven modeling in the realm of human neuroscience, give an overview of common tools of the trade, and highlight key advances in the literature. These tools have the potential to uncover critical insights in human neural function, as well as enable novel technologies beyond what is achievable with more traditional methods. Importantly, we discuss caveats and limitations of data-driven approaches, especially the dangerous blind use of black-box methods and the ethical ramifications of models that impact our sense of self.

A primer on data-driven models

What is a model? We can think of a model as a representation of reality; in the context of understanding human neuroscience and advancing neuroengineering applications, the most useful models are quantitatively rigorous and intimately tied to measurement data. In other words, models are representations of data that can be useful for recognizing patterns, making predictions, or controlling systems.

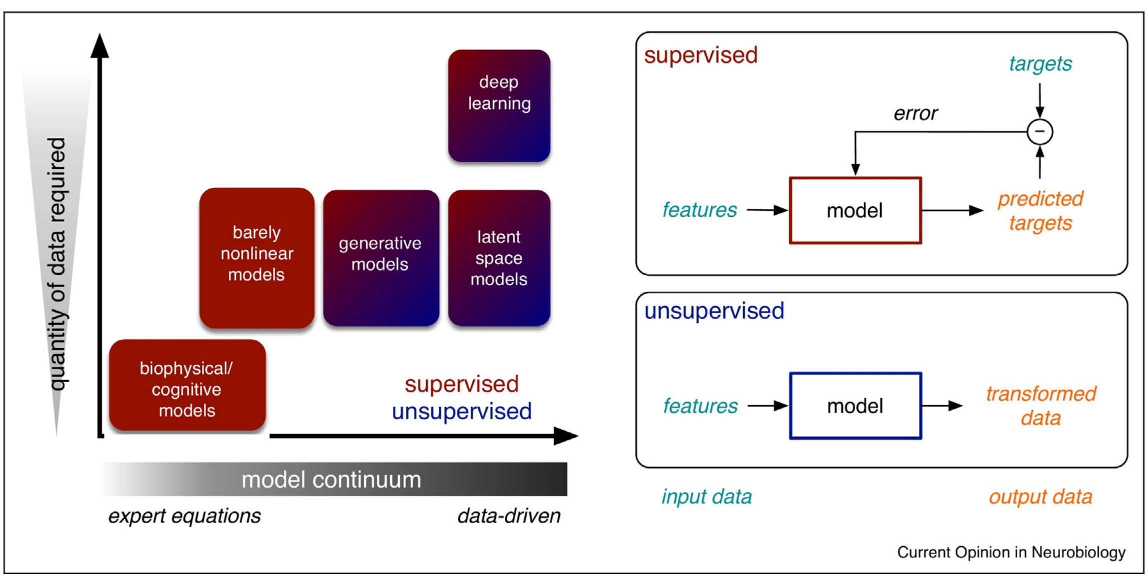
The choice of models best fit for a particular problem depends on a variety of factors, including how much data have been recorded and how much expert knowledge is available. This model continuum is shown schematically in Figure 1, and brief definitions of the key terminology are in Box 1. At one end of the continuum, equations are written based on existing theory of biophysics or cognition; these equations codify known relationships and dependencies between variables and features. Example models of this type include the Hodgkin-Huxley model of a spiking neuron [4] and the drift-diffusion models of short-term memory and decision-making [5].

Data-driven models make increasingly few assumptions about the nature of the underlying system to be represented. Instead of relying on expert knowledge, relationships among measured features in the data are derived from the data. Common examples include generalized linear models, Bayesian generative models, and latent space (i.e. latent variable) models. Depending on the magnitude and nature of the assumptions made, this class of models typically require a moderate amount of training data. An increasingly popular class of highly flexible models are artificial neural networks. Although these

Box 1 Data-driven modeling terminology

machine learning: learning from data with computational algorithms. The blanket term can be used to refer to many types of modeling methods typically developed in statistics, computer science, and applied mathematics.input data: the data supplied by the user for fitting a model, including the features x and the targets y, if any. outputs: what a model produces. The nature of the desired outputs determines the type of model most appropriate for a specific task (see Figure 2).continuous outputsare numerical in nature, either ordinal or real valued. Examples include spiking rates, magnetoencephalography (MEG) activation, and intensity of auditory stimulus. categorical outputsare discrete in nature; members of different categories have no intrinsic similarity relationship. Examples include experimental block and neuron cell type.supervised models: a type of model where the outputs are predictions based on the input features x fit to the input targets y.targets y: in supervised models, these are ground-truth labels for each sample of the data. The model parameters are fit so that the outputs reproduce y as closely as possible, as defined by an error metric.unsupervised models: a type of model where the outputs are transformations of the input data that reveal some otherwise hidden structure in the features.discriminative modelstry to find a direct mapping function f from features x to targets y (i.e., $y = f(x)$). In the probabilistic setting, this approaches involves modeling the posterior probability $p(y|x)$ directly.generative modelstry to predict y from x by estimating the joint distribution $p(x, y)$, so that the prediction $p(y|x)$ can be indirectly obtained by applying Bayes' rule. Consequently, generative models can in principle produce synthetic, never observed examples by sampling from the estimated joint distribution.

Figure 1



A schematic of the continuum between models relying on expert knowledge and more flexible, data-driven models, showing roughly the quantity of training data required for each type. Fitting expert equations requires relatively little data and leads to more simply interpretable models; however, data-driven models are more expressive and able to uncover unexpected patterns in the data. Although we are showing the models to occupy distinct locations on these axes, we would like to emphasize the continuous nature of these models; for instance, not all latent space models are more data-driven than all generative models. We elaborate on each of these types of models in Section 'Highlights of data-driven discoveries'. We also color each type of model by whether they are supervised or unsupervised. A model can be conceptualized as a machine that takes input data and produces output data. Box 1 defines commonly used terms in data-driven modeling.

models have roots in connectivism, the recent success of deep neural networks (i.e. *deep learning*) to solve previously intractable problems has relied on the sheer size and complexity of both the networks and the training data [6].

We can also characterize types of models by whether they are *supervised* or *unsupervised* methods, which are models fit with or without ground truth (target) labels, respectively (Figure 1, right). In supervised models, a proper choice of input data—the features and targets—is essential to the success and usefulness of the resultant model. Further, the same measurements can be used either as features or as targets for different purposes. For instance, a decoding model takes neural activity as input features to decode the target behaviors; alternatively, an encoding model takes stimulus as input features to reproduce the target neural activity. In the absence of targets, unsupervised models transform the input data by discovering latent relationships or coherent dimensions in the features. Figure 2 outlines the decision process for choosing among types of data-driven models and gives a few simple examples of each type.

Highlights of data-driven discoveries

In this section, we review recent examples of data-driven models, roughly in order of increasing model complexity. Because biophysical and cognitive models assume substantial expert knowledge and leave relatively few free parameters, fitting them to physiological, imaging, psychophysical, or symptomatic measurements requires relatively little data. Therefore we focus this review on the more data-driven parts of the modeling continuum.

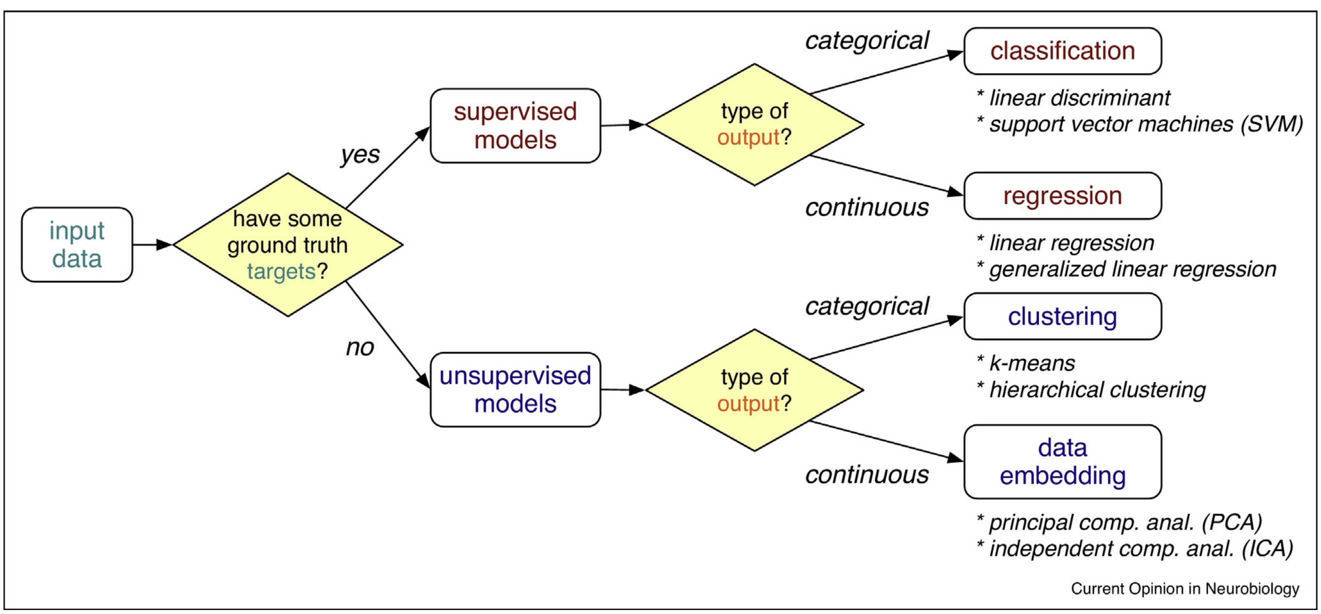
For each type of model, we highlight recent results from three different application domains: neuroimaging, single-neuron or neuronal population responses, and devices neuroengineering. In addition, we also focus on recent models that incorporate heterogeneous, multimodal data streams.

Barely nonlinear models

The field of neuroscience has a long tradition of attempting to capture underlying structure in data with simple, relatively rigid models that contain a fixed number of parameters. These simple models often start with an assumption of *linearity*; in other words, the inputs and outputs are related by a linear function, such that doubling the inputs would double the outputs. For instance, the response characteristics of neurons in early sensory pathways are traditionally modeled by a linear-nonlinear-Poisson (LNP) cascade model [7,8]. Although LNP models include a nonlinearity, their functional behavior is remarkably linear over their dynamic range. For the purpose of this review, we will therefore refer to these models as barely nonlinear models (BNMs).

Data-driven approaches are common in studies of human neuroanatomy and resting state networks, but they are

Figure 2



The decision process for choosing categories of data-driven models suitable for a particular task. Choices are based on whether some ground truth targets are used to fit the model, and whether the type of desired model outputs are categorical or continuously valued (see Box 1). Colors are consistent with what are used in Figure 1. We give two simple methods that exemplify each type of model. Further, some modeling frameworks (e.g., neural networks and latent space models) can fall under multiple types, depending on how they are structured and trained.

only beginning to be used in functional magnetic resonance imaging (fMRI). Functional imaging studies often assume that blood-oxygen-level-dependent imaging (BOLD) responses are due to a linear combination of causes [9,10]—known as the *general linear model* for fMRI, and not to be confused with the generalized linear models. More recent work has focused on extensions of the linear regression framework; for example, stimuli are first encoded into meaningful, potentially nonlinear features, and each voxel's responses are then regressed to these features [11••].

Another influential BNM in fMRI research is the population receptive field (pRF) method [12], which assumes that the response of each voxel has a specific parametric form (e.g., defined by stimulus orientation, eccentricity, or size). This allows pRF profiles to be measured directly by back-projecting preprocessed fMRI time series to the stimulus (e.g., [13,14]). In clinical neuroscience, BNM have recently been used to reveal functional reorganization of pRF in patients with schizophrenia [15] and autism spectrum disorders [16,17]. One advantage of pRF is that they provide a clear test of how well a model of voxel tuning preferences can predict BOLD responses; however, more recent work has shown that pRF profiles in some areas might not be easily parameterized [18•,19], motivating model-free approaches [18•]. In addition, only a few recent models have integrated heterogeneous data streams [20].

In device neuroengineering, BNM loosely inspired by information processing in the retina were used to fit a wide range of heterogeneous psychophysical data to predict visual outcomes in retinal prosthesis patients [21,22]. A complementary approach simulated neuronal activity using a biophysically detailed model of the retina, and then inferred the visual information available to the patient via optimal linear reconstruction [23]. These models have the potential to advance the state-of-the art in engineered devices to restore sight by unifying single neuron responses with perception.

Despite their wide use, the ability of BNM to capture cognitive and neurobiological processes is limited. Although BNM models are typically interpretable and require little data to fit their parameters, they are likely to underfit increasing quantities of rich neuroscience data [24].

Generative models

Generative models are often used to jointly estimate a brain-behavior relationship by using a hidden representation useful for explaining the target behavior. Common generative models include Bayesian networks and hidden Markov models (HMMs). Unlike deterministic models, generative models obtain a prediction by applying Bayes' rule to the joint distribution of the prediction problem (see Box 1). In this way, Bayesian models are calibrated on already existing, *prior* expert knowledge.

One approach to studying "effective" connectivity in brain imaging is via dynamic causal modeling (DCM) [25,26], a method to quantify the functional influence a particular brain region exerts on other brain regions. DCM affords an internal representation of how external inputs (i.e., known changes in experimental manipulation) lead to unobserved states of neuronal population responses, which in turn are assumed to generate the observed BOLD responses. DCM has been widely used to model sensory perception [27,28], analyze resting state [29•], and infer connectivity changes in various brain disorders [30,26]. In addition, a recent implementation of DCM in the frequency domain has made it possible to efficiently operate on large-scale brain networks [29•].

By exposing the low-dimensional structure embedded within high-dimensional brain measurements, generative models can provide interpretable and detailed insights into behavior and its disturbances. For example, HMM models of high-dimensional time-series data can infer the spatiotemporal topography of networks in response to the environment [31,32]. Another study used HMM to detect stable and abstract event boundaries in higher-order brain areas without relying on human annotations [33]. By integrating some BNM into a Bayesian framework, a HMM combined with regression was used to identify semantic maps for natural speech [34].

Beyond classification and regression, an important strength of generative models is that they are able to test hypotheses about how the observed data can be generated [35]. Many generative models assume some hidden structure that underlie the data, making them more reliant on expert knowledge than the latent space models discussed in the next subsection.

Latent space models

Latent space models (LSMs) have played a key role in furthering our understanding of high-dimensional neural population activity (for a recent review, see ref. [36]). LSM assume that n measurable variables, such as the spiking activity of a population of n neurons, are actually due to r unobserved, independently acting variables, called *latent variables* or *hidden causes*, where $r \ll n$. These latent variables define an r-dimensional space that represents the shared activity patterns prominent in the population response. Popular LSM include factor analysis, principal component analysis (PCA), and independent component analysis (ICA), which are unsupervised techniques, although supervised LSM are also commonly used.

LSM make it possible to integrate data collected using different recording techniques, such as fMRI and magnetoencephalography (MEG) [37], or the combination of brain imaging and behavioral data [38,39]. In clinical neuroscience, LSM are increasingly being used to predict patient outcomes [37,40]. Often, it is necessary to develop new methods to cope with the heterogeneity of these data sources, which has led to the development of a variety of probabilistic [41••,42•], multi-scale [43], and dimensionality reduction techniques [44,45].

In functional imaging, LSM have been used to probe brain states underlying vision [46], memory [47], resting states [48], mood [49], and various cognitive tasks. For example, human cognitive processes were shown to be influenced not only by external task demands, but also by latent, mental processes that change over time [50••,42•].

In device neuroengineering, LSM are useful to manage the dimensionality and complexity of the measured data. Recent examples include predicting cochlear implant outcomes from neuroanatomical data [51], making BCI control robust to future neural variability [52], and predicting human operator error in a BCI [53].

Moreover, control-theoretic approaches have impact beyond engineering and have also been useful to answer basic neuroscience questions about learning and adaptation. A key insight was a finding that different computations are carried out in different subspaces of neural population activity (termed the *intrinsic manifold*) [54,55]. This notion of a low-dimensional subspace was interrogated with a BCI to discover constraints on learning, explaining why some tasks are more easily or quickly learned than others [56,57••].

LSM are powerful tools in the analysis and modeling of high-dimensional data, especially those that involve several levels of abstraction or types of data. However, LSM often involve some hyper-parameters (e.g., the number of components or intrinsic dimensionality of the system) that must be specified by the investigator. In order to discover increasingly complex relationships among the available data, more flexible *non-parametric* models may be needed.

Deep learning models

Deep learning refers to a class of very large, multi-layered neural network models [6]. In contrast to expert equations and simple parametric models, deep learning models typically make weak assumptions about the data. This flexibility allows them to both automatically identify meaningful features and adapt their expressive capacity to the underlying complexity of the data. Modern DNN excel at hierarchical nonlinear classification and regression; in theory, they can represent any underlying distribution. The practical tradeoff is that the amount of training data required may be astronomical. Indeed, the tremendous success of recent DNN in different application domains is partly due to training sample sizes of $n>$ 1,000,000 [6]. In contrast, today's reference datasets in brain imaging reach between $\sim$1,000 participants in the Human Connectome Project to $\sim$10,000 participants in the UK Biobank Imaging Study. Dataset size alone has made it difficult to deploy state-of-the-art DNN in functional imaging studies.

Nevertheless, several studies have been able to circumvent the vast amounts of imaging data needed to train modern DNN architectures. These strategies include using a DNN with pre-trained weights [58] and augmenting existing datasets with synthetic data points [59,60]. However, by far the most popular approach is to train DNN on the input stimulus distribution instead of the recorded brain responses [61]. Other studies went a step further and argued for a close correspondence between simulated activity in individual layers of a convolutional neural network (CNN) and neuronal activity across the hierarchy of the visual system, either measured by fMRI [62•,63••] or by MEG [64,65].

Deep learning has also been used to solve neuroengineering tasks. For example, CNN have been able to increase performance in decoding electroencephalography (EEG) for movement [66,67], and recurrent DNN have made progress toward reconstruction of speech from intracranial EEG [68••,69,70,71]. Using both video and intracranial recordings, a multi-modal CNN combined video with intracranial neural recordings to decode and predict human movement in naturalistic contexts using thousands of examples of movement over hundreds of hours [72••]. In cochlear implant research, DNN are widely used for noise reduction to improve speech intelligibility [73] and music perception [74].

Deep learning is well suited for analyzing complex, multimodal data, including processing functional imaging data and controlling neuroprosthetic devices. Importantly, although the quantity of training data required is large and model fitting can be very processor intensive, the execution of a trained model on streaming data is relatively computationally tractable (e.g. [75]). However, due to the vast amounts of data required to train current DNN, their adoption in the domains of human neuroscience and neuroengineering is still emerging.

Open challenges and outlook

Human neuroscience faces a paradigm shift precipitated by rapid advances in the ways we acquire, manage, share, and understand data. Even so, for data-intensive discoveries to have their full impact, we must tackle a variety of key challenges in technology, training, and ethics.

Interpretability and generalizability. A pressing challenge is developing data-driven models that not only perform well but also give some insight into *how* they work. Simple parametric models are typically more interpretable, easier to implement, and faster to estimate, making them the best choice in data-scarce applications. However, they can often underfit the available measurements in data-rich scenarios. It has been argued that the reliance on parametric analysis may keep neuroscience from discovering novel neurobiological insights that surface only with more complex data representations [1]. Nevertheless, the "black box" nature of many data-driven methods, especially ones with many millions of parameters like modern DNN, impedes their adoption by scientists. In addition, since human neuroscience is intrinsically closely tied to translation, it is imperative that computational models yield insights that are are explainable to, and trusted by, clinicians, end-users, and industry. We suggest that the development of interpretable machine learning methods, including those that partially "bake in" known theory and expert knowledge, will be a fruitful focus of future research.

Training. The next generation of human neuroscientists will have access to genomic, anatomical, neural, and behavioral data of unimaginable richness and complexity. To take full advantage of these data, we need researchers who are fluent in the language of machine learning and adept in the practice of data science [76,2]. A transdisciplinary approach to academic training will be integral to producing, in Ed Lazowska's words, "π-shaped" individuals [77], who have deep expertise in both human neuroscience and in data science.

Ethics. The information age is awash in data, and the proliferation of machine learning tools applied to any and all data has produced some spectacular answers to questions that ought never have been asked. The academic literature and popular scientific news are rife with examples of data-driven models that amount to digital phrenology. In data-driven science as in all of science, asking the right questions can be the most crucial—and often the most difficult—part of a study. In conceptualizing machine learning models as schematized in Figure 1, we suggest that posing questions grounded in known hypotheses and theories is critical for making meaningful insights, in large part by using suitable input data, choosing models that make defendable assumptions, and asking for reasonable output types. Further, the technical community benefits enormously from continued and integrated engagement with the bioethics community [78]. We must be cognizant of the growing promise for great societal good as well as for deep invasions into our inner mental lives.

Will recording larger and higher resolution data produce fundamentally new insights in human neuroscience and advance neuroengineering? Here we have highlighted some recent work in the field that have made important strides in the right directions, but the answer to the big question is far from clear. Even so, it is plain that data-driven techniques will become increasingly prevalent in the near and intermediate future. We are optimistic that the continued development of modern computational techniques will shed light on mechanisms of human neural function in new and unexpected ways.

Conflict of interest statement

Nothing declared.

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