

# How to optimize neuroscience data utilization and experiment design for advancing primate visual and linguistic brain models?

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In recent years, neuroscience has made significant progress in building large-scale artificial neural network (ANN) models of brain activity and behavior. However, there is no consensus on the most efficient ways to collect data and design experiments to develop the next generation of models. This article explores the controversial opinions that have emerged on this topic in the domain of vision and language. Specifically, we address two critical points. First, we weigh the pros and cons of using qualitative insights from empirical results versus raw experimental data to train models. Second, we consider model-free (intuition-based) versus model-based approaches for data collection, specifically experimental design and stimulus selection, for optimal model development. Finally, we consider the challenges of developing a synergistic approach to experimental design and model building, including encouraging data and model sharing and the implications of iterative additions to existing models. The goal of the paper is to discuss decision points

**Abbreviations:** ANN: artificial neural network, AI: artificial intelligence, EEG: electroencephalogram, fMRI: functional magnetic resonance imaging

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and propose directions for both experimenters and model developers in the quest to understand the brain.

#### KEYWORDS

neuroscience, artificial neural networks, model development, data collection, vision, language

## 1 | INTRODUCTION

A core objective of neuroscience is to deepen our mechanistic understanding of the brain, which can be accomplished by developing computational models as explicit hypotheses. In recent years, many studies have focused on testing the accuracy of artificial neural network (ANN) models in matching primate behavioral and neural data, across the domains of vision (e.g., [1, 2, 3, 4, 5]), audition (e.g., [6, 7, 8, 9]), and language processing (e.g., [10, 11, 12, 13, 14, 15, 16]). In most of these cases, neural data have primarily been used to test whether ANN model responses match the brain responses using linear regression-based approaches (e.g., [2, 17]) or representational similarity analyses (e.g., [18]). However, recent studies have also demonstrated that primate neural data can be directly used (at various levels of abstraction) to finetune and optimize ANNs both to improve their match to brain responses as well as downstream task performance. For instance, simulating a primary visual cortex by matching the ANN front-end to empirically observed V1 properties improves robustness to image perturbations [19] while also better explaining higher-level visual cortical responses [20]. Similarly, [21] statistical properties of V1 activation patterns can serve as a teacher signal for training ANNs with resulting improvement in object recognition. More direct approaches include optimizing ANNs to align their representations to empirically observed neural responses in the macaque inferior temporal (IT) cortex, which has been shown to produce more primate-aligned, adversarially robust models of object recognition [22]. Related approaches have been proposed for language where language models can be modified to match brain activity better with resulting improvements in natural language processing tasks [23]. Another approach involves direct fine-tuning of language models on brain data, leading to improved brain predictivity performance, assessed through a different recording modality than the one used for fine-tuning [24]. These novel uses of neural data carry substantial promise for improving neural network performance and model alignment with primate neural and behavioral responses.

This article addresses two main challenges in the field of “NeuroAI” (intersection of neuroscience and artificial intelligence, AI; [25]). Both of these challenges focus on optimal model *development*, in contrast to model *evaluation* (e.g., [26]). **The first challenge concerns data usage in model development.** Fundamentally, do we believe it is the right time in neuroscience to use neural data to optimize models directly? Some neuroscientists [27, 28] (also see **Figure 1**) believe that we are still in the dark ages of neuroscience, which would suggest that more lay-of-the-land (exploratory) work needs to be conducted before we can begin collecting data at the granularity required to optimize model building directly. **The second challenge concerns future data collection efforts.** Should we rely on experimenter intuition derived from qualitative inferences generated by previous studies in the field, or should we use increasingly popular ANN-driven techniques such as the generation of “controversial” or “optimal stimuli” [29, 30, 31, 32] to guide experimental design? By addressing these challenges, we aim to develop more efficient ways of using neural data to build ANN models of the primate brain.

To set the stage for the two challenges, we first provide a brief review of the standard practices and recent advances in neuroscientific data collection, model development, and evaluation in visual and language neuroscience. We then elaborate on the challenges (“controversial axes”) and evaluate the pros and cons associated with each axis. Furthermore, a key aim of the article is also to address how experimentalists and modelers could interact most productively going forward: For researchers who are in a position to collect data, how should they be using models to inform their experiments, and similarly for researchers who build models, how should they engage with experimentalists?

## 1.1 | Data and model interaction in neuroscience

The field of neuroscience has undergone a foundational shift with the emergence of task-optimized ANN models, offering computational accounts of neural processes. Although models have been central to scientific cycles of data collection and knowledge refinement for centuries, the capabilities afforded by the new class of ANN models differ from traditional approaches (e.g., ANN models are “stimulus computable” [33] and can provide quantitative predictions for arbitrary stimuli). In this section, we provide a brief review of interactions between data and models in neuroscience.

In vision research, early experiments by Hubel and Wiesel [34, 35] used microelectrodes to record the activity of individual neurons in the visual cortex of cats and monkeys. They found that these neurons responded selectively to specific visual features, such as particular orientations of light. Based on a combination of anatomical and physiological findings, Felleman and Van Essen [36] proposed that the visual cortex is a distributed hierarchical processing system. In addition, many studies have further discovered various aspects about these brain areas [37, 38, 39, 40, 41], generating inductive biases that form the basis of the development of the hierarchical model of visual processing, which proposes that visual information is processed in a series of stages, with simple features detected in early stages and more complex features detected in later stages. With advances in computational techniques and refinement of questions, specific information about functional topographies [42, 43, 41], recurrent processing [4, 44], and other aspects of visual processing [45] has been incorporated in the architecture and computational motifs of the latest models of primate vision [46, 47, 48, 49, 50, 51, 52]. In addition, recent techniques have demonstrated using neural data to directly fit or regularize computational models [53, 22].

In language research, a set of frontal and temporal brain regions were identified as being implicated in language production and perception based on studies of patients with brain damage in the late 19th century [54, 55]. The evidence from brain lesions led to a family of descriptive models known as the “Classical model” or the “Wernicke-Lichtheim-Geschwind model” [56, 57, 58]. This family of models was later claimed obsolete due to, e.g., lack of definition of the brain regions described by these models (Broca’s and Wernicke’s areas) as well as the conflation of speech and linguistic processing [59]. Later evidence from linguistics and neuroimaging led to the proposal of several descriptive models of language processing (e.g., [60, 61, 62, 63]) which coarsely tie brain regions to particular cognitive process (“syntactic structure building” or “lexical access”). These models offered intuitive explanations of language processing but were based on words rather than mathematical or computational terms and did not provide quantitative predictions of neural responses to language. Behavioral research in psycholinguistics led to computational models of some aspects of linguistic processing. Examples of such models are surprisal-based models that posit that the degree of contextual predictability modulates language processing difficulty (e.g., [64, 65]). However, most of these models were limited by fixed vocabularies, methodological challenges in representing features associated with model internals, and only instantiated one specific hypothesis (e.g., about surprisal modulating behavioral or neural responses). Modern language models [66, 67, 68], in contrast, can provide representations for any arbitrary linguistic input with its preceding context, capturing various linguistic regularities through high-dimensional vectors (e.g., [69, 70]). These language models have provided the field with a chance to build quantitative models of neural processes for language. In addition, empirical evidence from neuroimaging further elucidated the brain regions implicated in language processing (the fronto-temporal language network; [71, 72, 73]), providing a clear target for modeling efforts. Multiple studies have now demonstrated that these modern language models can explain neural responses in the language network with unprecedented accuracy (e.g., [10, 11, 12, 13, 14, 15, 16, 74]).

## 1.2 | Advances in neuroscience data collection

Recent years have seen significant advances in neuroscience data collection, opening up new opportunities for model development using types and amounts of data that were previously unattainable. For behavioral data, online crowdsourcing platforms have enabled the collection of large labeled behavioral datasets (e.g., [75, 76] at a scale that has previously been unattainable. Many labs have developed similar home-cage kiosks that facilitate high-throughput

behavioral data collection in non-human primates [77, 78, 79]. Improved neural recording techniques now enable simultaneous measurements of hundreds or even thousands of neurons in awake, behaving animals across several levels of spatial and temporal specificity, such as multi-unit spiking activity [80, 81] or in-vivo calcium imaging [82]. Human neuroscience has also witnessed notable improvements in non-invasive fMRI data acquisition and analysis, including the use of high field strengths for acquisition (e.g., 7T), and analysis pipelines targeted towards modeling of event-related designs which provide fine-grained neural responses to each experimental trial [83]. Additionally, there has been a growing trend towards collecting massive amounts of data from a small number of individuals ("deep data" approach, e.g., [84, 85, 86, 87]). An example of such a dataset within the vision sciences is the Natural Scenes Dataset (NSD; [87]), which provides high-quality brain responses from a relatively low number of individuals to tens of thousands of images across diverse categories. The popularity of NSD demonstrates the hunger for reliable neural targets for model benchmarking at a fine grain across diverse stimuli, as opposed to data collected for specific hypotheses to broad stimulus categories (e.g., high vs. low contrast images or sentences vs. lists of words).

Further, direct brain perturbation strategies can be utilized to guide hypothesis testing (and related data collection) in both animals [44, 88, 89, 90] and humans [91, 92, 93]. Brain perturbations can leverage predictions from quantitative models to modulate brain activity according to a desired target [94, 30, 31, 95, 32]. Apart from the acquisition of neural responses to these coarse-grain brain perturbations [90, 96], the past decades have seen significant advances in more targeted genetic methods for collecting neural data in an even more targeted manner. Two key techniques are optogenetics [97] and chemogenetics [98], which allow researchers to selectively activate or inhibit specific neurons or circuits in the non-human primate brain, establishing causal relationships between neural activity and behavior. In summary, recent advances in data collection, from large-scale behavioral datasets via online platforms to sophisticated neural recording techniques and targeted neural perturbation techniques, hold immense potential for developing novel types of models and refining existing ones.

### 1.3 | Advances in computational brain model development

The last decades have seen significant advances in the development of computational models for neuroscience, particularly in the fields of vision and language. In the field of vision, the development of computational models has been motivated by empirical findings on receptive fields [34, 35] and hierarchical cortical processing [36], computationally formalized by Fukushima as the Neocognitron [99]. Improvements to this basic structure led to the development of the HMAX model [100]. A significant breakthrough was attained about a decade ago when it was discovered that convolutional neural networks that achieve human-level visual categorization performance quantitatively predict neural responses [2, 101] and representational structure[1] in high-level visual cortex in non-human primates and human primates, respectively. In addition, they also allow precise control of neural activity [30, 31], making them promising tools for clinical translation. Similarly, in the field of language, models have evolved from n-gram [102, 103] and distributional semantics models (e.g., [104, 105, 106]) to Transformers (e.g., [66, 67, 68, 107]), which have shown great success in natural language processing tasks such as text generation, question-answering, translation, summarization, and language-based reasoning (e.g., [108, 109, 110, 111]). These model advancements provide a new set of explicit hypotheses about how the brain processes visual and linguistic information and constrain models of the brain by quantitatively predicting from the raw sensory inputs the resultant brain activations. Interestingly, leveraging the transformer architectures that have been successful in language, vision transformers [112] also seem to improve performance in visual recognition tasks.

In this article, the primary class of models that we engage with (with respect to the data from Section 1.2) are those that are stimulus-computable, highly performant in the task/behavior of choice, and falsifiable (i.e., make explicit, testable predictions). In addition, we aim to have interpretable model components besides the input and output [113], which can provide insights into the neural mechanisms implicated in the behavior. By engaging with these types of models, we can better understand the relationship between neural activity and behavior and make progress in developing more accurate and interpretable models of brain function. In addition, we consider model development

within two different neuroscientific domains: vision and language. Until now, most modeling efforts have targeted each domain separately, but we anticipate increasing focus on integrating these modeling efforts (see Section 1.4).

## 1.4 | Considering an integrative approach to developing computational models of visual and linguistic cognition

At first glance, computational models of visual and linguistic cognition might appear very different from one another. Why, then, might we want to consider these two seemingly different domains in discussions related to model development? We believe that shared insights between visual and linguistic models should represent a productive path for modeling efforts in less studied domains and for developing multi-componential models encompassing several perceptual/cognitive systems in a single, integrated model that links from one perceptual/cognitive process to another. For instance, one obvious point of link between vision and language systems is reading, which serves as a promising testing framework for models that integrate processing in the visual ventral stream with language processing in the fronto-temporal language areas. Another direction involves leveraging visual and linguistic modalities simultaneously to better explain responses in brain areas implicated in “higher-level” visual function or semantic processing through multi-modal models (e.g., [114]) [112]. Finally, insights from one domain might help the other domain. For instance, linguistic models can help characterize and interpret visual models [115, 116]. Below, we briefly summarize the current commonalities and differences between computational modeling of visual and linguistic cognition.

## 1.5 | Commonalities and distinctions in computational modeling of visual and linguistic cognition

As mentioned above, several similarities and differences exist in approaches to modeling visual and linguistic processing. One major similarity is that task-optimized models tend to predict neuroscience data well in both visual and linguistic domains. For example, in the visual domain, models that perform the task of object recognition better (typically using ImageNet [75]) also better predict neural activity in areas of visual cortex involved in object perception [2, 1, 117] (but see [118]). In the linguistic domain, models that are better at predicting the upcoming word also better predict brain activity during language processing [12, 13, 119] (but see [120]). Another commonality is the presence of geometric phenomena in both visual and linguistic models. Specifically, both domains have shown evidence of “untangling” properties where semantically related information [121, 122] become more efficiently organized in high-dimensional space.

On the other hand, one difference in the research approaches when modeling vision and language is the availability and use of human versus animal models. Visual studies have often leveraged the high temporal and spatial specificity available from invasive studies done in non-human primates, while linguistic studies rely primarily on human participants using non-invasive recording modalities (and coarser grain of brain measurements). Another difference is the level of domain knowledge required for modeling. In the visual domain, there is a wealth of knowledge about the structure and function of the visual system [123] that can be leveraged to inform models [118]. In contrast, there is less well-established domain knowledge in language processing, making the development of models with qualitative priors more challenging.

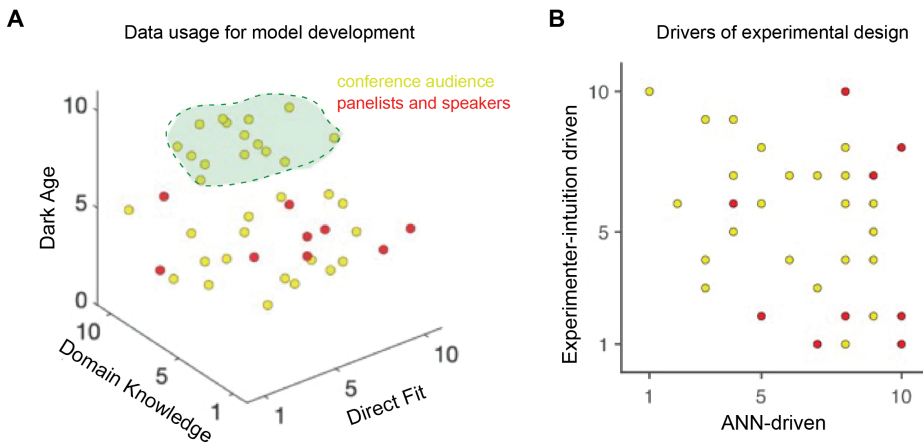
Below, we attempt to tailor our arguments to vision and language processing studies independently, wherever possible.

## 2 | THE CONTROVERSIAL AXES

As neuroscience continues to evolve rapidly (under limited resources [124]), researchers need to adapt their strategies to make the most of existing data, design effective experiments, and develop models that accurately capture the

complexity of the brain. Addressing these high-level challenges produces certain issues (denoted as “controversial axes” in this article) that warrant careful consideration.

Below, we elaborate on the specific challenges and controversial aspects that formed the basis of our discussions during the Generative Adversarial Collaborations (GAC) session of the Conference on Cognitive Computational Neuroscience [125], 2022, structured as follows: Each sub-section opens with a “controversial” claim, then proceeds to an explanation of the approach proposed by the claim. Each sub-section provides supporting arguments for the proposed approach and concludes with a box that outlines counterarguments or key considerations to keep in mind.



**FIGURE 1** Audience and GAC participant poll results. Each dot shows the rating provided by the conference audience (in yellow) and the GAC panelists and speakers (in red) to three positions. 1 - Do not agree at all, 10 - Strongly agree. **A.** Answers to the following three opinions. **Direct Fit:** “Experimental data (not insights from “textbooks”) should be used to directly train artificial neural network models of brain activity and behavior.” **Domain Knowledge:** “Qualitative insights (and not experimental data) from previous and existing experimental results should be used (e.g., as inductive biases) to design artificial neural network models of brain activity and behavior.” **Dark Age:** “We are still in the dark ages of neuroscience, and more lay-of-the-land type (“fundamental”) neuroscience work needs to be conducted before we start collecting data at a grain leveraged for building artificial neural networks of brain activity and behavior.” The green-shaded region highlights a mismatch between the ratings from the audience and the GAC speakers. Unlike the speakers, the audience felt that neuroscience is still very much in its early days, and data collection optimized for model development might be a premature idea. **B.** Answers to the following two opinions. **ANN-driven:** “Experimental design should be based on artificial neural network models that are predictive of brain activity and/or behavior (for designing and optimizing experimental paradigms using, e.g., ‘controversial’/‘optimal’ stimuli).” **Experimenter-intuition driven:** “Experimental design should be based on neuroscientists’ intuition derived from qualitative inferences generated by previous studies in the field (e.g., V1 cells like oriented bars, let’s find out what V2 cells like).”

## 2.1 | How do we optimally utilize neuroscience data for model development?

### 2.1.1 | Qualitative insights (not raw experimental data) from experiments should be utilized to design ANN models of brain activity and behavior.

#### Qualitative insights

In neuroscience, existing assumptions and knowledge about a brain area or specific mechanisms can be used to build ANN models without necessarily engaging with all the experimental data collected to develop this knowledge base. This approach incorporates inductive biases based on qualitative insights from existing experimental results. Examples

of these insights include the hierarchical processing of information in the visual cortex [126, 41, 37, 42, 38], recurrent processing [4, 44, 127], nonlinear properties of neural activity, spatial (e.g., retinotopy, [128, 129, 130, 131]) and functional specialization (e.g., face-selective neurons) [132, 42], short and long time-scale adaptation [133, 134] among others. Arguably, the success of the current CNNs as models of primate vision [33, 135] can be attributed to such model architectures being influenced by decades of inductive biases from the primate visual neuroscience and psychology literature (see discussions in [118]). Conversely, recent progress in the development of large-scale language models [68, 67, 136, 107], which also serve as state-of-the-art models of language processing in humans (e.g., [12]) arguably demonstrates that successful models do not always require insights from neuroscience.

### Arguments supporting this approach

Employing a scientific approach based on qualitative insights offers several advantages. Qualitative insights allow for the abstraction of general concepts into the form of inductive biases within ANN models. Importantly, such concepts lack idiosyncrasies of any given neuroscience dataset and/or recording modality. Incorporating general concepts of perceptual/cognitive functions explicitly in models in the form of inductive biases is a direct way of testing if that factor is important to account for the relevant neuroscientific data, improving our “understanding” of the brain. In a regime where data are limited, qualitative insights are the only resource to develop and advance models. Qualitative insights, e.g., recurrent processing, can be instantiated in a series of (very different) models [46, 47] and can subsequently be benchmarked against empirical data and compared to models developed using other insights (e.g., feedforward processing with constrained topographic organization, [50, 49]). The summary of these outcomes can drive broad trajectories of future models.

#### Things to keep in mind

The decision process of which insights to incorporate into a model is not trivial, and it is important to ensure that the chosen inductive biases are causally important and not merely epiphenomenal. There is an ongoing debate about the relative merits of direct fit versus inductive biases in model development (e.g., [137, 138]).

### Definition of terms.

**Making progress in neuroscience:** Building falsifiable, quantitatively accurate brain models leads to progress in visual and linguistic cognition.

**Neuroscience data:** Neuroscience data includes both neural data, such as data obtained from electrophysiology or brain imaging techniques, and behavioral data, such as data obtained from perceptual or psychological experiments.

**Benchmarks:** A quantitative measure of how well a brain model can predict empirical neuroscience data.

**Inductive bias:** Inductive bias refers to the set of assumptions or prior knowledge built into the design of a machine learning algorithm or artificial neural network (ANN). In neuroscience, inductive bias can be considered the set of constraints or assumptions based on our understanding of the brain and how it processes information.

**Direct fit:** Direct fit refers to fitting a model to empirically measured neuroscience data by directly optimizing the model's parameters to minimize the difference between the model's predictions and the empirical neuroscience data.

**Animal (in-vivo) model:** Animal (in-vivo) model refers to using living animals (e.g., rhesus macaques) as a model system to study neural function and behavior to make inferences about neurobehavioral aspects in another species (e.g., humans).

**Computational (in-silico) model:** Computational (in-silico) model refers to using computer simulations (e.g., deep convolutional neural networks, large language Transformer models) of behavior and neural function to make inferences about neurobehavioral aspects in another species (e.g., humans).

**Prediction:** Prediction refers to the ability to quantitatively forecast or anticipate neural activity in a brain region or behavior in a specific task.

**Control:** Control refers to the ability to perform closed-loop manipulation of neural activity and behavior through optogenetic, electromagnetic, chemogenetic, or pharmacological interventions.

**Understanding:** Understanding in this context refers to the ability to create falsifiable computational models to make accurate predictions, provide a basis for control, and explain underlying neural mechanisms via model components that are interpretable to experimenters.

## 2.1.2 | Experimental data (not qualitative insights from “textbooks”) should be used to directly train ANN models of brain activity and behavior.

### Quantitative insights

Using large-scale behavioral and neural experimental data to train ANN models directly represents an emerging approach in neuroscience research. In this approach, behavioral or neural signals are a rich source of information to learn better algorithms from, either directly or indirectly. The most straightforward approach is to train models to directly predict behavioral or neural responses. Another approach is to leverage neuroscientific data indirectly, e.g., as part of the loss function for models trained to perform a normative task (e.g., [139]). In neuroscience, there has been a long tradition of using statistical methods, such as Poisson likelihood, to fit likelihood-based models directly to neural spike trains, and modern ANNs fit naturally in this framework. The current best models of early visual areas, such as the retina and primary visual cortex in mice and monkeys, have been developed using this approach [140]. Various other recent studies [22, 141] have demonstrated the effectiveness of directly optimizing models on experimental data for higher visual cortices. Consideration of the various forms in which neuroscientific data can be directly integrated with a model's training regime, e.g., in the form of abstractions of data like representational dissimilarity matrices [142], can lead to better models of behavior and brain activity.

The tradition of incorporating quantitative insights is less prevalent in language compared to vision, but studies



[143, 144, 24, 145] have made efforts to leverage neuroscientific data for language-based tasks such as sentiment analysis or relation detection.

**Arguments supporting this approach**

Data-driven ANNs, trained using specific neural population activity or behavioral patterns, offer a direct way to develop models of targeted behaviors or brain areas. Direct fit to neuroscientific data can provide shortcuts to a more accurate representation of the mechanisms for the behavior of interest or response patterns in the targeted brain area. This approach can provide a complementary strategy of model development that does not rely on computational search for the optimal architecture, loss function, and task to develop a goal-directed ANN that, in turn, might have internals with brain-aligned representations. Although data limitations exist when fitting directly to neuroscientific data, combining data across multiple experimental sessions can help overcome this challenge [146]. Compared to the inferences abstracted (and therefore compressed) as qualitative insights, direct fitting, when performed in a data-rich regime, is likely to be free of the biases introduced by the cognitive capacity of a human experimenter. In other words, this approach helps to avoid experimenter bias in the interpretation of results, as feeding data directly into the model may expose it to factors that are not immediately interpretable to a human experimenter.

**Things to keep in mind**

The success of direct fitting is strongly dependent on the scale and richness of the available neuroscientific data. The nature of the data used for training significantly influences a model's predictive capabilities. For example, training predominantly on static images like those from ImageNet limits the ability to predict dynamic stimuli, such as naturalistic motion. This highlights the need for diversifying training data to enhance the scope and accuracy of model predictions. Furthermore, even with ample data, there is inherent tension between fitting large expressive models and smaller, biologically constrained models that are more prone to local minima. Integrating various types of neuroscientific data, such as single units and voxels, across different species on the same stimulus set could provide invaluable insights. If a single model can explain data across these modalities and species, it might reveal a universal principle of brain organization. Conversely, if adjustments are needed to accommodate humans and non-human primates, it could offer insights into how these brain systems differ. Therefore, assessing the type, diversity, and sufficiency of data is crucial. Developing theoretical tools for this assessment will significantly determine the suitability of the approach for model development, ensuring that the models not only fit well but also are representative and capable of making accurate predictions across various stimuli and neuroscientific contexts.

**2.2 | How do we optimally design future experiments?**

**2.2.1 | Experimental design should be based on neuroscientists' intuition derived from qualitative inferences generated by previous studies in the field**

**Model-free experimental design**

Traditionally, the field of neuroscience has relied heavily on both theoretical and incremental experimental work to guide experimental design and the selection of appropriate experimental stimuli. In the current work, we define "model-free" as designing experiments by choosing the experimental stimuli based on the experimenters' intuitions about the outcome ("Brain region A responds more to images of images of curved surfaces" or "Brain region B responds more to ambiguous words than unambiguous words"), without the use of an explicit computational model. Thus, model-free experiments only generate qualitative, descriptive predictions. In principle, there is also an implicit model leveraged in this case. But the model essentially runs in the experimenters' heads instead of predictions derived in-silico

("model-based"), making quantification of progress intractable.

In vision neuroscience, model-free approaches broadly fall into three categories: i) hand-constructed stimuli based on prior experimental evidence and experimenter intuition [34, 35, 147], ii) stimuli that are amenable to linear systems analysis or another systems identification approach [148, 149, 150], iii) natural stimuli (either fully naturalistic, e.g., [151, 152], or augmented to represent rare stimuli occurrences, e.g., [153] or constructed to contain the statistical structure of natural images e.g., Najemnik and Geisler (2005) [154]. In language neuroscience, "traditional" (i.e., model-free) approaches for deriving stimuli for experiments broadly fall into two categories: i) hand-constructed stimuli based on psycholinguistic evidence, theoretical constructs, and/or experimenter's intuition (e.g., [155, 156, 157, 158, 63]), ii) stimuli sampled from naturalistic corpora (either fully naturalistic as, e.g., [114] or 'deceptively' naturalistic as for instance [159, 160] where stimuli are constructed to contain an over-representation of rare stimuli occurrences than would otherwise be embedded in fully naturalistic stimuli distributions).

### Arguments supporting this approach

Model-free approaches for deriving experimental stimuli can, in some cases, provide several advantages, including interpretability, explicit control of confounding factors, and inclusion of infrequently occurring phenomena (e.g., [159, 160, 161], as elaborated below.

One key advantage is interpretability: Experimenters can choose stimuli directly linked to a descriptive, model-free hypothesis being tested, making it tractable to interpret results and draw conclusions, albeit limited by the boundaries of what humans can explain and put into words. Hence, if the experimental outcome falls within the possible scenarios hypothesized by the experimenter, the experiment provides a degree of abstraction in understanding the link between stimuli and outcome in the brain region. Interpretability, in combination with the experimenter's ability to reason about potential confounds and stimulus properties that are uninteresting to the hypothesis being tested, allows for even more targeted investigations of the phenomenon of interest. Another key advantage of experimenter-derived stimuli is the ability to include rare phenomena. Within language, some linguistic phenomena are rare albeit useful for investigating mechanisms of language processing [162, 163]. Language models are trained to generate the most plausible next word given the preceding context. If stimuli are derived directly from these models, they will likely miss out on these less common phenomena. In contrast to experimenter-designed stimuli, with natural stimuli, a strong argument can be made that they should be used because they contain the relevant input statistics for the system that evolved to process them [164].

### Things to keep in mind

While model-free stimulus selection is often based on the experimenter's targeted hypotheses, it also encompasses a wider range of choices that typically may not be considered as hypotheses. A prominent example is the use of stimuli with statistical properties of natural sensory input [165], which can also be considered an experimenter's intuition-driven set of stimuli. However, it is an intuition grounded in the assumption that an accurate brain model should similarly process naturalistic input as the primate brain (e.g., [166]). Stimuli derived for neuroscience experiments based on strong top-down assumptions of the experimenter often come with strong expectations of finding parallels between the hypothesized representations and organization of the brain. For example, within vision, it was hypothesized that motion detection in the primate brain involves temporal delays due to intrinsic differences between fast (magnocellular stream) and slow synaptic transmission (parvocellular stream). However, despite strong expectations of finding a relationship between the expected temporal delay circuits in the brain and motion perception, the empirical evidence has been questionable [167, 168]. Similarly, within language, a large body of theoretical work focused on the distinction between syntax (form) and semantics (meaning), and the expectation was a parallel organization in the brain. Later studies showed a lack of empirical support for this distinction [169, 170, 63, 171]. These two examples demonstrate that neural populations might be tuned to many (possibly interacting) dimensions related to the stimulus, which are not immediately intuitive or interpretable to the experimenter.

## 2.2.2 | Experimental design should be based on artificial neural network models that predict brain activity and/or behavior

ANN models can be effectively used in designing and optimizing experimental paradigms, for instance, through "controversial" or "optimal" experimental stimuli. We define a "model-based" approach as one where experiments (and stimuli) are designed using explicit computational models that offer hypotheses in the form of quantitative predictions about the experimental outcome. In its most conservative form, such a framework posits that one should not design an experiment without explicit, quantitative predictions from a computational model. It is important to note that by model-based stimulus selection, we do not imply using sophisticated machine learning-based tools (e.g., generative models) to derive stimuli for experiments that are otherwise based on an experimenter's intuitive hypotheses. In a model-based approach, the computational model itself serves as the hypothesis. These models/hypotheses are stimulus-computable and make precise predictions for each stimulus. This approach is similar in principle but distinct from stimuli generation strategies used in previous studies based simpler, non image-computable models [147, 172].

To make the process of falsifying or validating the models more efficient, the models themselves can be used to generate stimuli: for example, models can be used to generate "optimal" stimuli, stimuli that predict a certain activation level in a location, e.g., maximal activation, in a group of neurons or a brain region [94, 30, 31, 173, 95]. Another example is to generate "controversial" stimuli, stimuli for which models produce maximally distinct predicted responses, to test discrepancies between models and humans [174, 29].

### Arguments supporting this approach

Model-based approaches for determining experimental design (including but not limited to stimuli) can provide several advantages, including efficiency and a computationally tractable way of expanding the hypothesis space. The space of all possible stimuli that one might use as experimental stimuli is infinite. Given that the models serve as the hypothesis being tested, one can leverage their predictions to efficiently select stimuli that will most efficiently discriminate among them. This is in sharp contrast to an approach where stimuli for model evaluation are either selected randomly or based on the experimenters' intuition. Experimenter-derived stimuli often come with strong assumptions about the experimental outcome, while relying on models that instantiate these expected outcomes allows us to generate stimuli

and associated predictions that are critical in efficiently falsifying such models and testing alternative theories. A model-based approach can help design experiments that allow us to test an expanded space of hypotheses in a more tractable manner than a model-free approach. For instance, using a model-based approach, Kar et al. (2019) ([4]) discovered specific images where primates outperformed the feedforward convolutional neural networks during object discrimination tasks, thereby exposing a large explanatory gap. This motivated the design of recurrent convolutional neural networks [4, 46, 47] aimed at specifically bridging this explanatory gap between primates and models. In summary, the model-based experimental design provides a tractable method for directly falsifying the model via its predictions, leading to a virtuous cycle of model falsification and improvement.

**Things to keep in mind**

Inferences based on model-based experimental approaches are limited by the existing biases, idiosyncrasies, and/or discrepancies of the current generation of models in the stimulus selection process. These biases might be challenging to identify due to the black box nature (lack of human interpretability; [113]) of most modern ANNs. Using existing classes of models to generate stimuli with subsequent model validation might increase our chances of validating the models instead of discovering novel, potentially more accurate models. Additionally, by using models to close the experimental loop, we may be overfitting conditions where artificial and biological networks are aligned (e.g., processing of images) at the cost of ignoring entire dimensions of relevance for vision (e.g., time).

**3 | GOING FORWARD: MAKING, MEASURING AND UNDERSTANDING PROGRESS**

In this concluding section, we discuss three issues related to optimal model development going forward. First, we discuss how to foster progress through data and model sharing. Next, we discuss how to measure progress through model evaluation. Finally, we discuss how to understand progress through theory and how theory can aid in developing better models.

**3.1 | Fostering progress: Data and models**

In this article, we have highlighted and discussed the approaches for optimal model development encompassing “traditional” experimental methods and more recent model-based techniques. However, a key challenge in enhancing collaboration between experimentalists and model developers lies in the sharing of data and models. To foster an environment conducive to data and model sharing, it is necessary to address technical, ethical, and policy-related issues. Technically, we should develop robust, secure, and user-friendly data infrastructures that support seamless sharing and collaboration, possibly utilizing advanced cloud technologies and decentralized systems. Regarding policy, fostering an academic culture and funding ecosystem that values and rewards data sharing will be critical. This approach involves implementing strong incentives around data ownership, access, and use for individual researchers and institutions to share their work. Also, standardizing data and model formats to ensure interoperability is critical. In addition, one must also carefully consider how data sharing for model development interacts with model evaluation. Certain datasets need to be stored privately (and regularly updated) by integrative benchmarking platforms (like Brain-Score, [175]) to ensure that the models are not directly fit on the test data. Finally, from an ethical perspective, it is critical to ensure privacy, confidentiality, and informed consent, especially when dealing with sensitive data, by establishing rigorous institutional protocols and legal agreements.

## 3.2 | Measuring progress: Model evaluation

This article has focused on model *development*, and not *evaluation*. However, development and evaluation are inherently connected, and a key question is whether model development will change as model evaluation changes. Current models are being developed and evaluated primarily using prediction-based measures such as regression [2]. Prediction-based metrics can be leveraged for neural control where model-based predictions are used to identify stimuli aimed at eliciting a particular response in neurons or brain regions [30, 32], providing a more robust test of the model's predictions.

Another avenue of evaluation includes metrics that take into account the geometry of neural populations or ANN unit activations, such as representational similarity [176, 177]. More recent approaches within geometric measures include manifold-based metrics, which allow for quantification of manifold dimensionality and separability of representations in high-dimensional neural and artificial populations [121]. Other recent geometry-based approaches include generalized shape metrics [178], pointwise representational similarity [179], or soft matching distance [180]. New evaluation measures are also being developed. For example, direct interfacing of brain responses into models [181] with subsequent evaluation of task performance represents an exciting direction within model evaluation. Another example is the direct comparison of responses to spoken language from the auditory brain stem recorded via electroencephalogram (EEG) and representations from generative audio networks [182], bypassing the transformations (e.g., via regression) that are typically used to evaluate the similarity between brains and models. Finally, several platforms now offer integrative benchmarking, which includes evaluation across a broad and diverse range of models, datasets, and metrics. Examples of such platforms are Brain-score [101], Algonauts [183, 184], and Sensorium [185] which all aim to provide a more comprehensive picture of the computational models' alignment with the biological brain irrespective of the idiosyncrasies associated with smaller scale evaluations.

## 3.3 | Understanding progress: Linking models with theory

In discussions about model development, it is not uncommon to note diverse opinions about the notion that “we need more theory”. In this section, we briefly discuss what we consider a theory and how linking model development with theory can lead to a fruitful cycle of model development.

A scientific theory (in neuroscience and general) synthesizes evidence, rationale, and ideas that help us explain empirical observations. They are tools by which scientists can:

1. Make sense of the observations, which typically involve mathematical formulations and abstractions of raw data using various statistical tools to understand the underlying patterns and structures (e.g., dimensionality estimates, manifolds, identifying specific spatiotemporal functional topographies).
2. Make predictions, which can be achieved by instantiating the theories as explicit computational models (like a trained neural network). These models allow for falsifiable predictions.

Given this broad definition of theory, we believe that theoretical work can be leveraged at various stages of model development, experiment design, and data collection. We emphasize that we view computational models as instantiations of theories, not theories per se. Some instances of the utility of theory are discussed below:

**When generating new hypotheses:** A robust theory can suggest novel and testable hypotheses. It can guide the instantiation of those hypotheses as explicit computational models. These models can then make predictions that explore new empirical data points that might have remained unexplored, ideally to falsify or discriminate amongst those same models.

**When integrating and interpreting data:** Theories can help in the mathematical formulation and abstraction of raw data, allowing scientists to discern patterns and structures that are not immediately obvious. The theoretical framework

can inform which statistical tools to apply and how to interpret their outputs. For instance, it has been empirically observed that classification accuracy of object category improves along the ventral visual hierarchy [80] of the primate brain and the hierarchies in the deep convolutional neural networks. Recent theoretical work [121] has explained how the changes in the geometry of the neural-population responses to an object category ("object manifold") can be quantitatively summarized with "classification capacities" and how the classification capacity-based estimates of the manifolds' radius, dimensionality, and inter-manifold correlations, can further explain the functional roles of different parts of this hierarchy.

**In refining experimental methods:** Theories can inform the design of experiments by predicting what conditions are most likely to yield informative results. This can optimize resource use and direct experimental efforts more efficiently.

**For iterative model-experiment cycles:** Theory-driven models can be used to generate predictions that are tested experimentally. The results of these experiments can, in turn, refine the theory, leading to a virtuous cycle of improvement in both theoretical understanding and model precision. Therefore, the mode of leveraging theory is likely cyclical.

**When validating a model's biological plausibility:** A theoretical understanding of the ANN models can ensure that they are not just fitting data but are also capturing the underlying biological processes at the right level of abstraction. A theoretical grounding could limit the domains in which the model predictions should be considered for empirical testing. For instance, while the backpropagation algorithm is widely used in the supervised training of ANNs, and the associated gradients approximated at each layer of the model hierarchy might indeed reflect a biologically relevant learning signal magnitude, it might not provide a direct neural mapping of how such gradients are implemented in the neural circuitry.

## 4 | CONCLUDING REMARKS

In the rapidly evolving field of NeuroAI, the integration of neuroscience data with computational model development offers exciting and promising directions in the modeling of brain function, yet it also presents several challenges and decision points. In this paper, we focused on i) optimal usage of neuroscientific data in model development, contrasting raw experimental data with qualitative insights, and ii) optimal data collection efforts, contrasting model-based versus model-free approaches to experimental design. The main scope of the paper is to formulate and discuss the different opinions (at each end of the spectrum) on the role of data usage and experimental design in model development. In doing so, we hope that the readers will recognize the assumptions and considerations underlying these decisions.

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