Abstract

Decoding behavior, perception, or cognitive state directly from neural signals has applications in brain-computer interface research as well as implications for systems neuroscience. In the last decade, deep learning has become the state-of-the-art method in many machine learning tasks ranging from speech recognition to image segmentation. The success of deep networks in other domains has led to a new wave of applications in neuroscience. In this article, we review deep learning approaches to neural decoding. We describe the architectures used for extracting useful features from neural recording modalities ranging from spikes to EEG. Furthermore, we explore how deep learning has been leveraged to predict common outputs including movement, speech, and vision, with a focus on how pretrained deep networks can be incorporated as priors for complex decoding targets like acoustic speech or images. Deep learning has been shown to be a useful tool for improving the accuracy and flexibility of neural decoding across a wide range of tasks, and we point out areas for future scientific development.

1 Introduction

Using signals from the brain to make predictions about behavior, perception, or cognitive state, i.e., “neural decoding”, is becoming increasingly important within neuroscience and engineering. One common goal of neural decoding is to create brain computer interfaces, where neural signals are used to control an output in real time. This could allow patients with neurological or motor diseases or injuries to, for example, control a robotic arm or cursor on a screen, or produce speech through a synthesizer. Another common goal of neural decoding is to gain a better scientific understanding of the link between neural activity and the outside world. To provide insight, decoding accuracy can be compared across brain regions, cell types, different types of subjects (e.g., with different diseases or genetics), and different experimental conditions. Plus, the representations learned by neural decoders can be probed to better understand the structure of neural computation. These uses of neural decoding span many different neural recording modalities and span a wide range of behavioral outputs.
Within the last decade, many researchers have begun to successfully use deep learning approaches for neural decoding. A decoder can be thought of as a function approximator, doing either regression or classification depending on whether the output is a continuous or categorical variable. Given the great successes of deep learning at learning complex functions across many domains [13–22], it is unsurprising that deep learning has become a popular approach in neuroscience. Here, we will review the many uses of deep learning for neural decoding. We will emphasize how different deep learning architectures can induce biases that can be beneficial when decoding from different neural recording modalities and when decoding different behavioral outputs. We hope this will prove useful to deep learning researchers aiming to understand current neural decoding problems and to neuroscience researchers aiming to understand the state-of-the-art in neural decoding.

2 Deep learning architectures

At their core, deep learning models share a common structure across architectures: 1) simple components formed from linear operations (typically matrix multiplication or convolution) plus a nonlinear operation (for example, rectification or a sigmoid nonlinearity); and 2) composition of these simple components to form complex, layered architectures. There are many formats of neural networks, each with their own set of assumptions. In addition to feedforward neural networks, which have the basic structure described above, common architectures for neural decoding are convolutional neural networks (CNNs) and recurrent neural networks (RNNs). While more complex deep network layer types, e.g., graph neural networks [23] or networks that use attention mechanisms [24], have been developed, they have not seen as much use in neuroscience. Additionally, given that datasets in neuroscience typically have limited numbers of trials, simpler, more shallow deep networks (e.g., a standard convolutional network versus a residual convolutional network [21]) are often used for neural decoding.

RNNs typically use a sequence of inputs. RNNs are also capable of processing inputs that are sequences of varying lengths, which occurs in neuroscience data (e.g., trials of differing duration). This is unlike a fully-connected network, which requires a fixed dimensionality input. In an RNN, the inputs are then projected into a hidden layer, which connects to itself across time (Fig. 1B). Thus, recurrent networks are commonly used for decoding since they can flexibly incorporate information across time. Finally, the hidden layer projects to an output, which can itself be a sequence (Fig. 1B), or just a single data point.

CNNs can be adapted to input and output data in many different formats. For example, convolutional architectures can take in structured data (1d timeseries, 2d images, 3d volumes) of arbitrary size. The convolutional layers will then learn filters of the corresponding dimensions, in order to extract meaningful local structure (Fig. 1C). The convolutional layers will be particularly useful if there are important features that are translation invariant, as in images. This is done hierarchically, in order to learn filters of varying scales (i.e., varying temporal or spatial frequency content). Next, depending on the output that is being predicted, the convolutional layers are fed into other types of layers to produce the final output (e.g., into fully connected layers to classify an image). In general, hierarchically combining local features is a useful prior for image-like datasets.

Weight-sharing, where the weights of some parameters are constrained to be the same, is often used for neural decoding. For instance, the parameters of a convolutional (in time) layer can be made the same for differing input channels or neurons, so that these inputs are filtered in the same way. This is analogous to CNN parameters being shared across space or time in 2d or 1d convolutions. For neural decoding, this can be beneficial for learning a shared set of data-driven features for different recording channels as an alternative to human-engineered features.

Training a neural decoder uses supervised learning, where the network’s parameters are learned to predict target outputs based on the inputs. Recent work has combined supervised deep networks with unsupervised learning techniques. These unsupervised methods learn (typ-
ically) lower dimensional representations that reproduce one data source (either the input or output), and are especially prevalent when decoding images. One common method, generative adversarial networks (GANs) \[25, 26\], generate an output, e.g., an image, given a vector of noise as input. GANs are trained to produce images that fool a classifier deep network about whether they are real versus generated images. Another method is convolutional autoencoders, which are trained to encode an image into a latent state, and then reconstruct a high fidelity version \[27\]. These unsupervised methods can produce representations of the decoding input or output that are sometimes more conducive for decoding.

3 The inputs of decoding: neural recording modalities and feature engineering

3.1 Neural recording modalities

To understand how varying neural network architectures can be preferable for processing different neural signals, it is important to understand the basics of neural recording modalities. These modalities differ in their invasiveness, and their spatial and temporal precision.

The most invasive recordings involve inserting electrodes into the brain to record voltages. This allows experimentalists to record spikes or action potentials, the fast electrical transients that individual neurons use to signal, and the basic unit of neural signaling. To get binary spiking events, the recorded signals are high-pass filtered and thresholded. Datasets with spikes are thus binary time courses from all of the recording channels (Fig. 1A). These invasive measurements also allow recording local field potentials (LFPs), which are the low-pass filtered version (typically below \(\sim 200\)Hz) of the same recorded voltage. LFPs are thought to be the sum of input activity of local neurons \[32\]. When all voltage is included across frequency bands, the voltage is generally referred to as wide-band activity. Datasets with LFP and wide-band are continuous time courses of voltages from all the recording channels (Fig. 1A). Note that traditionally, due to the distance between recording electrodes being greater than the spatial precision of recording, spatial relationships between electrodes are not utilized for decoding. Spikes, LFP, and wide-band are more commonly recorded from animal models than humans because of their invasive nature.

Another invasive technique for recording individual neurons’ activities is calcium imaging, which uses microscopy to capture images of fluorescent calcium indicators that are sensitive to neurons’ spiking activity \[33\]. The raw outputs of calcium imaging are videos: pixels measure fluorescence at the times when, and locations where, neurons are active. Calcium imaging is only used with animal models.

Electrical potentials measured from outside of the brain, that is electrocorticography (ECoG) and electroencephalography (EEG), are common neural recording modalities used in humans. ECoG recordings are from grids that record electrical potentials from the surface of the cortex, require surgical implantation, and often cover large function areas of cortex. EEG is a non-invasive method that records from the surface of the scalp from up to hundreds of spatially distributed channels. Like LFPs, datasets from ECoG and EEG recordings are continuous time courses of electrical potentials across recording channels (Fig. 1A), but here the spatial layout of the channels is also sometimes used in decoding. Note that as these electrical recording methods get less invasive, spatial precision decreases (from spikes to LFP to ECoG to EEG), which can lead to inferior decoding performance \[34, 35\]. Still, all these electrical signals can be recorded at high temporal resolution (100s-1000s of Hz) which make them good candidates for fast time-scale decoding.

Magnetoencephalography (MEG), functional near infrared spectroscopy (fNIRS), and functional magnetic resonance imaging (fMRI) are also noninvasive recording modalities which are most often used in human decoding experiments. MEG measures the weak magnetic fields that are induced by electrical currents in the brain. Like EEG and ECoG, MEG can be recorded with high temporal precision. fNIRS and fMRI measure blood oxygenation (a proxy for neural
Figure 1: Schematics. A: Schematics of neural decoding, which can use many different neural modalities as input (top) and can predict many different outputs (bottom). Embedded figures are adapted from [28–30]. B: A schematic of a standard recurrent neural network (RNN). Each arrow represents a linear transformation followed by a nonlinearity. Arrows of the same color represent the same transformations occurring. The circles representing the hidden layer typically contain many hidden units. More sophisticated versions of RNNs, which include gates that control information flow through various parts of the network, are commonly used. For example, see [31] for a schematic of an LSTM. C: A schematic of a convolutional neural network. A convolutional transformation takes a learned filter and convolves it with the input (here, a 2d input), and then passes this through a nonlinearity. This means that here, a $2 \times 2$ filter will be multiplied pixel-wise with all $2 \times 2$ blocks to get the values of the next layer in the network.
activity), through its absorption of light and with resonance imaging respectively, and their temporal resolution are temporally limited by its dynamics. fNIRS and fMRI datasets contain activity signals in different voxels (locations) of the brain over time. Due to the limited temporal resolution, sometimes the temporal continuity of this data is not used for decoding purposes (Fig. 1A).

### 3.2 Feature engineering

For each of these recording modalities, the raw data are processed to create features that are beneficial for decoding. Sometimes, these features are hand-engineered based on previous knowledge, traditionally with the goal of creating features that are most compatible with linear decoders. Other times, this feature engineering is part of the deep learning architecture. That is, a more raw form of the input is provided into the decoder, and a first stage of the deep network decoder will automatically learn to extract relevant features. Specific neural network architectures can be beneficial for this automatic feature engineering (Fig. 2).

For use in decoding, spikes are typically first converted into firing rates by determining the number of spikes in time bins. Then, these firing rates are fed into the decoder. This general approach of decoding based on firing rates (an assumption of “rate coding”) is standard. While using precise temporal timing of spikes (“temporal coding”) for decoding has been done [36], we are not aware of examples using deep learning. Given that firing rates are used as inputs, additional neural network architectures are not used to extract unknown features from the input. However, in future research, it might be advantageous to provide a more raw form of spiking as input, and use deep learning architectures to do feature engineering. For rate coding, the best
size and temporal placement of time bins could be automatically determined, and for temporal
coding, features related to the precise timing of spikes could be learned.

When analyzing calcium imaging data, the videos are typically preprocessed to extract time
traces of fluorescences over time for each neuron \[37\]. Sometimes, additional processing will be
done to estimate spiking events from the calcium traces \[38\]. Deep learning tools exist for both
of these processing steps \[39, 40\]. For decoding, either the fluorescences, or the estimated firing
rates (via the estimated spike trains), are then used as input. While it could be possible to
develop an end-to-end decoder that works with the videos as input, this may prove challenging
given the potential for overfitting with high-dimensional input.

When decoding from wide-band, LFP, EEG, and ECoG data, it is common to first extract
spectrottemporal features from the data, for example the signals in specific frequency bands.
Sometimes, only “task-relevant” frequencies will be used for decoding - for instance, using
high gamma frequencies in ECoG to decode speech \[41, 42\] (Fig. 2A). More frequently, many
frequencies will be included, to better understand which are contributing to decoding \[12, 43\].
Similar to frequency selection based on domain knowledge, ECoG grid electrodes and fMRI
voxels are often subsellected by hand or with statistical tests. In general, these extracted features
can then be put into almost any type of decoder, such as linear (or logistic) regression or a deep
neural network (e.g. \[44\]).

It is also possible to let a deep learning architecture do more of the feature extraction. One
approach is to first convert each electrode’s signal into a frequency domain representation over
time (i.e., a spectrogram), often via a wavelet transform. Then, this 2-dimensional representation
(like an image) is provided as input to a CNN \[35, 45–47\] (Fig. 2B). If multiple electrode channels
are being used for decoding, each channel can be fed into an independent CNN, or alternatively,
the CNN weights for each channel can be shared \[35\]. The CNN will then learn the relevant
frequency domain representation for the decoding.

Another approach is to provide the raw input signals into a deep learning architecture
(Fig. 2C). To learn temporal features, typically the signal is fed into a 1-dimensional CNN,
where the convolutions occur in the time domain. This has been done with a standard CNN
\[48\], in addition to variant architectures. Ahmadi et al. \[49\] used a temporal convolutional net-
work, which is a more complex version of a 1-dimensional CNN that (among other things) allows
for multiple timescales of inputs to affect the output. Li et al. \[50\] used parameterized versions
of temporal filters that target synchrony between electrodes. These convolutional approaches
will automatically learn temporal filters (like frequency bands) that are relevant for decoding.

In addition to temporal structure, there is often spatial structure of the electrode channels
that can also be leveraged for decoding (Fig. 2A). Convolutional filters can be used in the spatial
domain to learn spatial representations that are relevant for decoding, for example local func-
tional correlation structure. It is common for the temporal filters and spatial filters to be learned
in successive layers of the network, either temporal followed by spatial \[51, 52\] or vice-versa \[53\].
Additionally, 3-dimensional convolutional filters can be learned that simultaneously incorporate
both temporal and (2-dimensional) spatial dimensions \[54\] or 3 spatial dimensions \[55\]. Including
spatial filters, which is most common in EEG and ECoG, can help learn spatial motifs that
are most relevant for the task. Moreover, from a practical perspective, convolutional networks
are an efficient way of processing high-dimensional spatial data.

4 The outputs of decoding

Neural decoding is used to predict many outputs, including movement, speech, vision, and
more. Sometimes, the output variable will be directly predicted from the neural inputs, e.g.,
when predicting movement velocities. Other times, the decoder may be trained to predict some
intermediate representation, which has a predetermined mapping to the output (Fig. 3). For
example, a GAN can be trained to generate an image using a small number of latent variables.
This mapping from the low-dimensional variables to images can be learned without having to
simultaneously record neural activity. Then, to decode an image from neural activity, one
can train the decoder to predict the latent variables to be fed into the GAN, rather than the entire high-dimensional image. This two-step approach can be especially beneficial when the output data is complex and high-dimensional, as is often the case in vision or speech. In effect, the generative model can act as a prior on the underconstrained decoding solution. Across the following decoding outputs, researchers have used both the “direct” and “intermediate mapping” approaches (Fig. 3).

4.1 Movement

Some of the earliest uses of neural decoding were in the motor system [56]. Researchers have used neural activity from motor cortex to predict many different motor outputs, such as movement kinematics (e.g., position and velocity), muscle activity (EMG), and broad type of movement. Traditionally, this decoding has used methods (e.g., Kalman Filter or Wiener Filter) that assumed a linear mapping from neural activity to the motor output, which has led to many successes [57–60]. To improve the decoders, these methods were extended to allow specific nonlinearities (e.g., Unscented Kalman Filter and Wiener Cascade [61–64]). Within the last decade, deep learning methods have become more common, frequently outperforming linear methods and their direct nonlinear extensions when compared (e.g., [28, 53, 65–66]).

Deep learning methods for decoding movement have been applied to a wide range of problems. Researchers have used many input signals that have high temporal resolution, including spikes [28, 65–70], wide-band [71, 72], LFP [44, 49], EEG [73, 74], and ECoG [53, 75–77]. Additionally, deep learning has been used to predict many different outputs. Often the output is a continuous variable, such as the position, angle, or velocity of a limb, joint, or cursor [28, 44, 49, 53, 65–69, 70, 73], or a muscles EMG [67] (Fig. 3B). Rather than predicting a continuous variable, sometimes the goal is to classify different movement types [71, 72, 74–77], for example, classifying which finger is moving [73]. Finally, deep learning decoders have been used to predict movements from effectors across different parts of the body, including arm [28, 44, 49, 65, 68, 70], leg [65, 69, 74], wrist [67, 71, 72], and finger movements [53, 71, 72, 75–77]. Thus, deep learning methods have shown to be a very flexible tool for movement decoding.

RNNs are by far the most common deep learning architecture for movement decoding. When predicting a continuous movement variable, there is generally a linear mapping from the RNNs output to the movement variable. When classifying movements, there is an additional softmax nonlinearity that determines the movement with the highest probability. From a deep learning perspective, given that this is a problem of converting one sequence (a temporal trace of neural activities) into another sequence (motor outputs), it would be expected that an RNN would be an appropriate architecture. Recurrent architectures also make sense from a scientific perspective: motor cortical activity has dynamics that are important for producing movements [78], plus movements themselves have dynamics.

LSTMs have generally been the most common and successful type of RNN for decoding [28, 44, 53, 65–67, 75–77], although other standard types of RNN architectures (e.g., GRUs [79] and echo-state networks [70]) have also proven successful. Additionally, researchers have found that stacking multiple layers of LSTMs [65, 75] can improve performance beyond a single LSTM [65]. LSTMs are likely successful because they are able to learn long-term dependencies better than a standard “vanilla” RNN [31].

A common goal of neural decoding of movement is to be able to create a usable brain computer interface for patients. While the majority of deep learning uses have been in offline scenarios (decoding after the neural recording), there are several successful examples of real-time uses of deep learning for movement decoding [66, 70, 72]. For example, in human patients with tetraplegia who had implanted electrode arrays, Schwemmer et al. [71] were able to classify planned movements of wrist extension, wrist flexion, index extension, and index flexion. They then applied functional electrical stimulation to activate muscles according to this decoder, so that the patient was able to make these movements in real time. In Sussillo et al. [70], monkeys with implanted electrode arrays were able to control the velocity of a cursor on a screen in real time.
Figure 3: Architectures and outputs of decoding. **A:** Sequential inputs can be processed by RNNs which can use past context (or past and future in bi-directional RNNs). **B:** RNN outputs at each timestep can be mapped to behaviors, e.g., movements, measured concurrently. **C:** The final output of an RNN can be used as the input to a decoding network which can produce a second sequence of a different length, such as text. **D:** RNNs can produce an intermediate state to be used in a second decoding step. **E:** Intermediate states can often be structured, such as a spectrogram in this example. **F:** Intermediate states can be fed into an acoustic model which produces acoustic waveforms. **G:** Image-like inputs can be processed by CNNs to produce intermediate feature vectors. **H:** Feature vectors can be fed into generative image models, e.g., a GAN, to produce a more realistic looking image.
While there has been great initial success, there are several challenges associated with using deep learning for real-time decoding for brain computer interfaces. One challenge is that the source of the recorded neural activity can change across days, for example due to slight movement of implanted electrodes. One approach that has dealt with this is the multiplicative RNN, which allows mappings from the neural input to the motor output to partially change across days [66]. Another challenge is computation time, as there is the need to make predictions through the deep learning architecture at very high temporal resolution. When using a less complicated echostate network, Sussillo et al. [70] were able to decode with less than 25 ms temporal resolution. However, when using a more complex architecture of LSTMs followed by CNNs, Schwemmer et al. [71] decoded at 100 ms resolution, slower than our perception. Relatedly, for linear methods that can be fit rapidly, researchers are able to adapt the decoder in real time to better match the subjects intention (trying to get to a target) to improve performance [58, 62]. Developing similar approaches for deep learning based decoders is an exciting, unexplored area.

4.2 Speech

Vocal articulation is a complex behavior that engages a large functional area of the brain to produce movements that have a high degree of articulatory temporal and spatial precision [79]. It is also a uniquely human ability which limits the recording modalities and neuroscientific interventions that can be used to study it. Due to the functional and temporal requirements of decoding speech, cortical surface electrical potentials recorded using ECoG is the typical recording modality used, although penetrating electrodes, MEG, EEG, and fNIRS are also used [80–83]. When decoding from ECoG or EEG, researchers commonly use the signals’ high gamma amplitude [41], although some use more broad spectrotemporal features as well [41, 43, 84].

Many approaches to decoding speech from neural signals have used some combination of linear methods and shallow probabilistic models. Clustering, SVMs, LDA, linear regression, and probabilistic models have been used with spectrotemporal features of electrical potentials to decode vowel acoustics, speech articulator movements, phonemes, whole words, and semantic categories [41, 43, 80, 85–88].

Deep learning approaches to decoding speech from neural signals have emerged that can potentially learn nonlinear mappings. Some of these approaches have operated on temporally segmented neural data and have thus used fully connected neural network architectures. For example, spectrotemporal features derived from ECoG or EEG have been used to reconstruct perceived spectrograms, classify words or syllables, or classify entire phrases [12, 42, 82–84]. These examples with temporally segmented neural data are useful for increasing understanding about neural representations, and as a step towards decoding natural speech.

Mapping directly from continuous, time-varying neural signals to speech is the goal of speech brain-computer interfaces [89, 90]. Both convolutional and recurrent networks are able to flexibly decode timeseries data and are often used for decoding naturalistic speech. Heelan et al. [91] reconstructed perceived speech audio from multi-unit spike counts from a non-human primate and found that LSTM-based networks outperformed other traditional and deep models. Speech represented as text does not have a simple one-to-one temporal alignment to regularly sampled neural signals. For this reason, speech-to-text decoding networks often use architectures and methods like sequence-to-sequence models or the connectionist temporal classification loss [20, 92], which are commonly used in machine translation or automated speech recognition applications. As such, several groups have decoded directly from neural signals to text using recurrent networks such as sequence-to-sequence models [93, 94] (Fig. 3C).

For decoding intelligible acoustic speech, it is also common to split decoding into a more constrained neural-to-intermediate mapping, followed by a second stage that maps this intermediate format into an acoustic waveform using acoustic priors for speech based on deep learning or hand-engineered methods. For instance, high gamma features recorded using ECoG have been used to decode spectrograms and speech articulator dynamics [54, 95] as intermediate states. Then, either a WaveNet deep network [96] was used to directly produce an acoustic waveform.
from the spectrogram [54], or an RNN was used to produce acoustic features which were fed into a speech synthesizer [55]. These second stages do not require invasive neural data for training and were trained on a larger second corpus.

Deep learning models have improved the accuracy of primarily offline speech decoding tasks. Many of the preprocessing and decoding methods reviewed here are done offline using acausal or high-latency deep learning models. Developing deep learning methods, software, and hardware for real-time speech decoding is important for clinical applications of brain computer interfaces [88, 97].

4.3 Vision

Similar to decoding acoustic speech, decoding visual stimuli from neural signals requires strong image priors due to the large variability of natural scenes and the relatively small bit-rate of neural recordings. Early attempts to reconstruct the full visual experience restricted decoding to simple images [98] or relied on a filterbank encoding model and a large set of natural images as a sampled prior [99]. Qiao et al. [100] solved the simpler task of classifying perceived object category using one CNN to select a small set of fMRI voxels which were fed into a second RNN for classification. Similarly, Ellis and Michaelides [101] classified among many visual scenes from calcium imaging data using feedforward or convolutional neural networks.

As mentioned in Deep learning architectures, deep generative image models, such as GANs, can produce realistic images. In addition, CNNs trained to classify large naturalistic image databases [102] (discriminative models) have been shown to encode a large amount of textural and semantic meaning in their activations [103], which can be used as an image prior. Due to the variety of ways that natural image priors can be created with deep networks, there exist decoding methods that combine different aspects of both generative and discriminative networks.

Given a deep generative model of images, a simpler decoder can be trained to map from neural data to the latent space of the model [104, 105], and the generative model can be used for image reconstruction. Similarly, a linear stage reconstruction followed by a deep network that cleans-up the image has been used with retinal ganglion cell output [27]. Generative models can also be trained to reconstruct images directly from fMRI responses on real data with data augmentation from a simulated encoding model [106].

Alternatively, generative and discriminative models can be used together. By leveraging a pretrained CNN, a simple decoder can be trained to map neural data to CNN activations that can then be passed into a convolutional image reconstruction model [107]. Additionally, the input image in a pretrained CNN can be optimized so that the CNN activations match predictions given by the fMRI responses [108]. Researchers have also used an end-to-end approach in which they train the generative part directly on neural data with both an adversarial loss and a pretrained CNN feature loss [109]. Along with acoustic speech, decoding naturalistic visual stimuli presents one of the best cases to study the use of data-driven priors derived from deep networks.

4.4 Other outputs

While we have chosen to focus on a few decoding outputs that are prevalent in the literature, deep learning has been used for a myriad of decoding applications. RNNs such as LSTMs have been used to decode an animals location [28, 35, 110, 111] and direction [112] from spiking activity in the hippocampus and head-direction cells, respectively. LSTMs have been used to decode what is being remembered in a working memory task from human fMRI [113]. Researchers have used LSTMs [114] and feedforward neural networks [115] to classify different classes of behaviors, using spiking activity in animals [116] and fNIRS measurements in humans [114]. LSTMs [116, 117] and CNNs [118] have been used to classify emotions from EEG signals. Feedforward neural networks have been used to determine the source of a subjects attention, using EEG in humans [119, 120] and spiking activity in monkeys [121]. CNNs [46–48], along with LSTMs [48]
have been used to predict a subject’s stage of sleep from their EEG. For almost any behavioral signal that can be decoded, someone has tried to use deep learning.

5 Discussion

Deep learning is an attractive method for use in neural decoding because of its ability to learn complex, nonlinear transformations from data. In many of the examples above, deep networks can outperform linear or shallow methods even on relatively small datasets; however, examples exist where this is not the case, especially when using fMRI [122, 123] or fNIRS data [124]. Relatedly, there are many times in which using hand-engineered features can outperform an end-to-end neural network that will learn the features. This is more likely with limited amounts of data, and also when there is strong prior knowledge about the relevant features. One general machine learning approach to efficiently use limited data is transfer learning, in which a neural network trained in one scenario (typically with more data) is used a separate scenario. This has been used in neural decoding to more effectively train decoders for new subjects [77, 94] and for new predicted outputs [71]. As the capability to generate ever larger datasets develops with automated, long-term experimental setups for single animals [125] and large scale recordings across multiple animals [126], deep learning is well poised to take advantage of this flood of data. As dataset sizes increase, this will also allow more features to be learned through data-driven network training rather than being selected by-hand.

Although deep learning will inevitably improve decoding accuracy as neuroscientists collect larger datasets, extracting scientific knowledge from trained networks is still an area of active research. That is, can we understand the transformations deep networks are learning? In computer vision, layers that include spatial attention [127] and methods for performing feature attribution [128] have been developed to understand what parts of the input are important for prediction, although the latter are an active area of research [129]. These methods could be used to attribute what channels, neurons, or time-points are most salient for decoding [128]. Additionally, there are methods for understanding deep network representations in computer vision that examine the representations networks have learned across layers [130, 131]. Using these methods may help to understand the transformations that occur within neural decoders, however results may be sensitive to the decoder’s architecture and not purely the data’s structure. While deep learning interpretability methods are not commonly used on decoders trained on neural data, there are a few examples of networks that were built with interpretability in mind or were investigated after training [12, 50, 51, 113].

When interpreting decoders, it is often assumed that the decoder reveals the information contained in the brain about the decoded variable. It is important to note that this is only partially true when priors are being used for decoding [132], which is often the case when decoding a full image or acoustic speech. In these scenarios, the decoded outputs will be a function of both neural activity and the prior, so one cannot simply determine what information the brain has about the output.

The software used to create, train, and evaluate deep networks has been steadily developed and is now almost as easy to use as other standard machine learning methods. A wide range of cost functions, layer types, and parameter optimization algorithms are implemented and accessible in deep learning libraries such as PyTorch or Tensorflow [133, 134] and libraries in other programming languages. Like other machine learning methods, care must be taken to carefully cross-validate results as deep networks can easily overfit to the training data.

In addition to their use in neural decoding, deep learning has other prominent uses within neuroscience [135, 136]. Neural networks have a long history in neuroscience as models of neural processing [137, 138]. More recently, there has also been a surge of papers using deep networks as encoding models [9, 11, 139]. There has been a specific focus on using the representations learned by deep networks trained to perform behavioral tasks (e.g., image recognition) to predict neural responses in corresponding brain areas (e.g., across the visual hierarchy [140]). Combining these multiple complementary approaches is one promising approach to understanding neural
computation.

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