Interpretability of statistical approaches in speech and language neuroscience

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Abstract

Brain functions are traditionally investigated using general linear models (GLM) in controlled experiments, which allow for a straightforward interpretation of the data. However, constraints imposed by controlled experimental setups have led neuroscientists to increasingly use machine-learning inspired approaches, which allow to work with large datasets collected in relatively natural experimental settings. Given the disparity of available methods and underlying concepts, synthesizing and relating the results of both traditional and machine-learning inspired experiments represents a substantial challenge. In this review, we propose to use a taxonomy based on the spatial specificity of the available methods and the extent to which they are constrained by a priori hypotheses, to classify their interpretability. Taking speech processing as a case example, we dissect the advantages and limitations of each of these methodological approaches, and highlight the ways in which they can be fruitfully combined to facilitate data interpretation.

/main text

The diversity of statistical approaches in cognitive neuroscience

A common experimental paradigm in cognitive neuroscience is to measure changes in neural activity in response to controlled manipulations of stimuli, tasks or behaviours. In these experiments, measured neural responses are generally analysed using a variety of statistical tests (e.g. t-test, F-tests, ANOVA) that are special cases of the so-called General Linear Model (GLM). These statistical analyses relate, at each point in anatomical space, the variance of neural responses with a set of pre-specified variables (predictors) which model the hypothesized effects of experimental manipulations and possible confounding factors. The GLM-based approach is well suited to test pre-defined hypotheses on the relation between specific components of cognitive and psychological models and the underlying functional neuroanatomy. In GLMs, the interpretation of the model fit to the data and the contribution of individual predictors is straightforward: predictors of the model are in small number and directly relate to controlled and a priori uncorrelated crafted experimental manipulations. In language research, for example, GLM-based studies have confirmed the important notion that speech and language-related cognitive operations emerge from processing hierarchies where each step has its own anatomo-functional specificity (Ding et al., 2016; Hickok & Poeppel, 2007; Sheng et al., 2018) (**Figure 1**, left panel).

Contrasting with this traditional paradigm, a more "naturalistic" approach has gained considerable traction in recent years (Poldrack & Yarkoni, 2016; Varoquaux & Poldrack, 2019). In these experiments, participants are presented with "real world" stimuli, with the goal of measuring how the brain responds to e.g. language "as it is used" (Hamilton & Huth, 2018). Neural responses collected using e.g. movies or audiobooks are often analysed using encoding models. In language research, encoding models have for example revealed semantic-category selective organization within broadly distributed brain regions ((Huth, de Heer, et al., 2016), **Figure 1**, middle panel). Similarly to GLMs, encoding models fit the neural responses univariately (i.e., voxel-by-voxel), with the goal of explaining/predicting the level of brain activity through the (linear) combination of a set of variables – typically, features of the stimuli. Interpreting the results of encoding

models is therefore more difficult than interpreting those of GLMs because the influence of each feature cannot be singled out, as the number of features might be large (in relation to the dataset), and the features might be correlated among them. This implies the use of various techniques (e.g. regularization, cross-validation) that further influence the estimated contribution of individual variables to the overall fitting. The interpretation of encoding analyses can hence benefit from comparing different stimulus representation models, with the assumption that the winning model reflects the actual neural representation (Santoro et al., 2014).

Unlike encoding models, decoding methods exploit the information in spatial patterns of neural responses and can be used to predict perception or behaviour (e.g. motor, speech output) or reconstruct the stimuli using the neural activity itself (Holdgraf et al., 2017). Decoding analyses rely on diverse machine learning techniques and can be broken down into (1) discriminative methods (e.g. classifiers), which aim at detecting multivariate differences between predefined task conditions or stimulus features (within small sets of voxels, regions, or the whole brain), and (2) model-based methods, which aim at reconstructing new stimuli or behaviours that are not present in the training set from brain activity, by predicting features of otherwise well-specified computational models, as in encoding (King et al., 2018). Note that encoding models can be used in conjunction with decoding models, often to optimize the performance of the latter (see (Naselaris et al., 2011, 2015), **Figure 1**, right panel). In language research, a recent study leveraged a model of the vocal system to decode the speech signal from the brain's response, making significant progress towards the possibility of restoring spoken communication in patients with paralyzing conditions (Anumanchipalli et al., 2019).

Several high-profile studies have recently highlighted the value of unsupervised clustering methods – e.g., dimensionality reduction techniques. Their most defining principle is to relax the constraints imposed by supervised, model-based approaches such as encoding/decoding. This allows a maximum of variance (or information) in the data to be accounted for by a combination of n non pre-specified dimensions (Brunton & Beyeler, 2019; Jack et al., 2018). Importantly, these unsupervised, data-driven methods (e.g. principal component analysis, PCA) do not use labels or specific information regarding the experimental design. Although these methods are often applied to conduct exploratory analyses on large data sets, they are also frequently used with the ambitious goal of discovering unpredicted representational and/or coding principles in the brain. This raises a number of issues that we attempt to expose in this article (see Behavioural relevance and functional specialization).

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the interpretation of results can be. In this review, we use this taxonomy to show that the difference in spatial specificity between methods, as well as the relative absence of biologically informed hypotheses, can lead to different interpretations of findings. We then describe different existing ways in which analysis approaches can be optimised to allow for more constrained interpretations of cognitive neuroscience research in the domain of speech and language, while at the same time capitalizing on the ability to exploit multivariate differences in the real world and/or uncover unpredicted organising neural principles.

Figure 2

Figure 2. A proposed taxonomy of statistical approaches/methods in cognitive neuroscience. The classification is based on two dimensions: (i) the “hypothesis-driven” dimension, which is characterised by a continuum between hypothesis- and data-driven approaches, i.e. between analysis methods that are to a greater or lesser extent guided by predefined assumptions (note that “data-driven” does not necessarily equate to “theory-free”); (ii) the spatial (anatomical) specificity of the approach: a univariate model considers a single spatial point at a time, whereas a multivariate model considers many spatial points at once, making the anatomical parcellation/interpretation of neural patterns more difficult.

Behavioural relevance and functional specialisation

Considerable efforts have been made in recent years to better understand how the brain forms concepts based on word meaning. One proposal is that cortical regions are organized in large-scale networks which both underpin semantic relations and support the emergence of higher-level concepts (Hagoort, 2014). Accordingly, and in parallel to classical hypothesis-testing experimental designs (Maess et al., 2016; Teige et al., 2018), studies using machine-learning inspired approaches have revealed a semantic-category

organization that is broadly distributed across the whole brain (Huth et al., 2012; Huth, de Heer, et al., 2016; Y. Zhang et al., 2020). Here, to characterize the semantic selectivity of each voxel, neural activity was measured with fMRI while participants passively listened to long narratives or watched natural movies. Neural activity parameters were fitted to semantic features using univariate linear regression (voxel-wise modelling), and the fitted model was projected onto a low-dimensional subspace obtained by applying dimensionality reduction techniques (e.g. principal component analysis, PCA). The resulting four dimensions were those that best explained the data. Importantly, no explicit assumptions were made regarding the combination of features that these four dimensions reflected. However, this raises some concerns related to the interpretation of the results. The inclusion of many independent variables (i.e., semantic features) requires strong post-hoc assumptions about the latent/underlying organisation of the resulting neural patterns, and some implicit assumptions might be incorrect. For instance, most studies implicitly assume that neuronal responses from any location in the brain can encode any representative semantic class, and that they do so based on locally specific functional recruitment patterns. Ideally, testing the specificity of these patterns would require to decode the same semantic features from neural activity at the same locations. Subsequent studies using such decoding methods, with maps based on the weight distribution across semantic labels, revealed less local semantic category specificity than expected (Huth, Lee, et al., 2016; Pereira et al., 2018). In these follow-up studies, each voxel of a given semantic map was associated with the meaning of few but semantically related words, suggesting a global 'map' of semantic categories with a broad distribution of semantic knowledge in the brain. It remains difficult, however, to reconcile these essentially descriptive conclusions with hierarchical processing where auditory input is progressively abstracted into higher-level language representations. The recent mapping of hidden units of deep architecture models with neuroimaging data speaks to such progressive abstraction process in natural language processing (Kell et al., 2018).

The multiple interpretations of data-driven dimensions

Finding out what information is contained in multivariate patterns arising from data-driven models is a necessary yet difficult task. Interpreting how neural data maps onto behavioural data or stimuli in an n-dimensional space requires dimensionality-reduction, which in turn leads to arbitrary interpretations since it relies on post-hoc interpretations regarding what each eigenvariate may represent. If no explicit hypothesis is formulated during the reduction of observed dimensions (i.e., during unsupervised procedures), the interpretation is uncertain. Each eigenvariate resulting from dimensionality reduction procedures describes a complex trajectory in a 4-dimensional (i.e., including time) state-space. Understanding what these trajectories represent and how they relate to the functional processing of specific regions is ultimately the hardest problem. If such trajectories are specific to functional regions, they might reveal the complexity/polyvalence of neural population coding, depending on task requirements (Rubin et al., 2019). However, if the sampled regions are ill-defined, e.g. when they are arbitrarily determined by cortical electrode grids or arrays used in the measurements,

these trajectories might reflect the mixed contribution of different computational levels resulting from multiple regions within the hierarchy (Roussel et al., 2020).

This point is well illustrated by a specific example in the speech literature. Using a data-driven approach (i.e., principal component and clustering analyses), Bouchard and colleagues identified patterns of spatially distributed neural activity in the human sensorimotor cortex during the production of consonant-vowel syllables (Bouchard et al., 2013). The authors proposed that these patterns reflect articulatory features, i.e., elementary speech motor sequences. Although this interpretation is reasonable, one may argue that an equally valid interpretation of the results is an organization that follows acoustic traits. The phonemic distribution in a 2D state-space highlighted by Bouchard (Linear Discriminate Analysis (LDA), Suppl. Fig. 10 in (Bouchard et al., 2013), **Figure 3A**) aligns surprisingly well with the spatial distribution of acoustic features described in 1969 by Jakobson, Fant, & Halle (pp. 33-348; see also **Figure 3B**, where consonants and vowels cluster along low/acute (LDA1) and compact/diffuse (LDA2) continua). Given the pivotal role of the somatosensory system in the hierarchical organisation of speech production (Franken et al., 2018), an organization based on combined acoustic and articulatory features provides the most likely interpretation for the phonemic topography emerging from neural activity in the ventral sensorimotor cortex (vSMC). This example illustrates that the same data-driven analysis can lead to very different interpretations, and that the conclusions that are drawn depend on the models that the experimenters have in mind and on the context in which results are interpreted (Bzdok et al., 2018). Unlike the hypothesis testing approach, the data-driven approach used in isolation ultimately leads to untested interpretations. In summary, and although it may appear counter-intuitive, the use of data-driven models requires extremely solid background hypotheses for post-hoc interpretation.

Can the brain exploit multidimensional features?

The choice of machine learning approaches in cognitive neuroscience implicitly contains the fundamental assumption that a given brain area can represent multiple features, and that these features can be captured by multivariate patterns. Yet, multivariate patterns may also capture phenomena other than locally processed features, such as, in particular, properties that are inherited from distant regions with which the sampled brain region interacts. For example, in patients with intracortical electrodes, it has been shown that the activity pattern identified in the ventral sensorimotor cortex (vSMC) corresponds to different articulatory features when the patients produced versus when they listened to syllables (Cheung et al., 2016). The authors argued that the neural response structure in the vSMC is organized according to “place of articulation” during speech production, but according to “manner of articulation” during speech listening, while the neural response in the STG is organized according to “manner of articulation” while both speaking and listening (Mesgarani et al., 2014) (**Figure 3C** and **3D**). When speech is perceived and then produced, the conversion of acoustic cues into motor routines involves the vSMC, which interfaces auditory and motor cortices (Assaneo & Poeppel, 2018; Liebenthal & Möttönen, 2017; Pulvermüller & Fadiga, 2010). Thus, we could argue here that the fact that articulatory features can be decoded similarly within the vSMC and the STG does not

unambiguously demonstrate that these regions encode or represent articulatory categories, but could equally mean that the structure of the articulatory space shares common properties with that of the acoustic space (see (Popov et al., 2018) for a similar point about shared variance in non-equivalent representational spaces). In principle, this isomorphism can be exploited by any “information-greedy” decoder to retrieve, in one representational space, the features that in fact only reflect meaningful dimensions in a different space. In this example, articulatory representations can be classified in a region known to encode acoustic features (the STG) simply because there is an (even partial) mapping between the acoustic and articulatory representational schemes, which causes their intrinsic representational properties to be correlated (Assaneo & Poeppel, 2018).

Figure 3

Figure 3. Differing interpretations depending on whether data collection is constrained by prior theoretically or biologically informed hypotheses. (a) and (b): comparison between the discriminant analyses in Bouchard et al., 2013 (Bouchard et al., 2013) with the acoustic features of Jakobson et al., 1969 (Jakobson et al., 1961). Bouchard et al. (2013) propose that these patterns (a) reflect articulatory features (i.e., elementary speech motor sequences), but an organization according to acoustic features (b) also provides a plausible interpretation of the findings. Images 3a & 3b courtesy of Michel Hoen and Willy Serniclaes. (c) In the STG (superior temporal gyrus), decoding patterns arising from machine learning algorithms show that the dimensions distinguishing the neural responses during listening and speaking are organized according to ‘manner of articulation’ cues. (d) In the vSMC (ventral sensorimotor cortex), decoding patterns show that neural responses are organized according to ‘manner of articulation’ cues during speech listening and according to ‘place of articulation’ cues when speaking. Fig. 3a adapted from

Bouchard et al., Suppl. Fig. 10, and Fig. 3b adapted from Jakobson et al., 1969, Figs. pp. 33-34.
Figures 3c & 3d adapted from Cheung et al., 2016 (Cheung et al., 2016), Figure 4 and Suppl. 2
Fig.

Optimizing multivariate analysis methods

Given the exploratory potential and also the interpretability issues of multivariate, machine-learning inspired approaches in cognitive neuroscience (Varoquaux & Thirion, 2014), it seems important to think about ways in which such methods can be capitalized on while at the same time limiting some of their pitfalls. One way to tackle this is to prioritize the use of model-based approaches, and as such to make them relatively more hypothesis-driven (De Angelis et al., 2017; King & Dehaene, 2014; Moses et al., 2016; Pasley et al., 2012). Furthermore, in particular in the domain of speech and language neuroscience, these models could be specifically tailored to the level(s) of the processing hierarchy and/or of the functional role of the region(s) being examined (Çelik et al., 2019; Deniz et al., 2019; Rutten et al., 2019; Venezia et al., 2019). Second, depending on the goal of the investigation, multiple models can be combined in order to question different levels of processing simultaneously (Anumanchipalli et al., 2019; de Heer et al., 2017), or applied separately to different functional subregions, based on the a priori hypotheses and predictions of the study (Kell et al., 2018). Third, again especially in speech and language neuroscience, it is primordial that modelling approaches take into account the dynamics of the signal, thereby constraining the search and thus also the interpretation space of machine learning approaches, this time in the temporal domain (Dichter et al., 2016; King & Dehaene, 2014; Loula et al., 2018; Moses et al., 2016).

We hence cautiously advocate that relating the output of multivariate analysis methods (i.e., multivariate patterns, state-space representations or classifier performance) to behaviour ought to involve the specification of tailored computation rules. For each possible task, and at each level of the processing hierarchy, there are optimal pre-informed ways of mapping the neural activity according to the variable of interest (Issa et al., 2018; Santoro et al., 2017). Known features of the functional hierarchy in the speech processing system could help to define an optimal algorithm, or a time-resolved model that varies depending on the processing stage (**Figure 4**). In visual perception, for instance, a geometric model can be defined whose features adapt to the known computational properties of each level of the functional hierarchy, from specific to general as one goes up towards more abstract levels (DiCarlo & Cox, 2007; Grill-Spector & Weiner, 2014; Nunez-Elizalde et al., 2018; van Gerven, 2017). For speech processing, to recover the function of the first two levels of the auditory hierarchy (Jiang et al., 2016; Santoro et al., 2017), it seems necessary to use models that take both the acoustic spectrum and time into account, with a spectro-temporal receptive field (STRF) model being more accurate in primary auditory cortex, and an STRF model tailored to phonological cues being more accurate in auditory association cortex (Dewitt & Rauschecker, 2012; Venezia et al., 2019). The same strategy may apply to higher-order regions where the natural dimensions of the feature space are less well known, i.e., semantic regions. At these levels of the processing hierarchy, linguistic representations are presumably a-temporal, encoded with sparse or rate codes (Chang et al., 2010;

Panzeri et al., 2010; Van Wassenhove, 2009; Q. Zhang et al., 2019). In this case, dimensionality reduction algorithms may leverage, together, various types of information, such as phonemic transitions, word probabilities or word transitions.

Figure 4

Figure 4. The importance of non-linear encoding in speech perception. Here we consider four processing stages in a very simple /ba/- /da/ categorisation task, each of them relying on the activation of a circumscribed area underlying a specific function. Along the processing hierarchy, time-based representations are gradually abstracted, from fine spectro-temporal decomposition in primary auditory cortex (PAC), to spectro-temporal encoding specific to phonological units in bilateral pSTG (posterior superior temporal gyrus), and phonological feature processing in the left pSTG, and finally to decisional processing in the left inferior frontal gyrus (IFG) (Bouton et al., 2018). Along the hierarchy, information is encoded through hierarchical, parallel and recursive processes (MacGregor et al., 2012; Strijkers, 2016). Representations are encoded within different time frames in the right and left pSTG; this is important to consider when using classification methods. A way to use machine-learning inspired methods within a hypothesis-driven approach would be, for example, to run multivariate-pattern and other forms of machine learning analyses on different types of measures selected based on the functional region they originate from, i.e., using STRFs at the lower levels of the auditory hierarchy (Rutten et al., 2019; Santoro et al., 2017), phonemic transitions in the left pSTG or word probabilities and transitions in the left IFG.

Such model-based decoding has been used to study how the auditory encoding of different acoustic dimensions is modified depending on whether people attend to linguistic (e.g. phonological) or para-linguistic (i.e. voice) information in pseudo-words (Rutten et al., 2019). Although in this study only an acoustic model was used for questioning the data, extensions to models containing e.g. pitch and higher level

phonemic features would allow to generate an ‘embedded’, or concatenated model space (de Heer et al., 2017). Here, it might be expected that different features (e.g., acoustic, phonological and pitch) best explain the neural data within different functional subregions of the auditory hierarchy and/or during different tasks, allowing to gain a broader understanding of how our auditory system makes use of linguistic and paralinguistic information in speech. Two recent fMRI studies having compared the performance of models targeting different processing levels (i.e. acoustic versus pitch (De Angelis et al., 2017) and spectral, articulatory and semantic (de Heer et al., 2017) illustrate how model-based machine learning approaches can be used to tap into different levels of the processing hierarchy, and to complement hypothesis driven approaches in revealing the regional functional specificity of these.

Approaches that deviate from the GLM experimental approach can be more fine-tuned for research on the neuroscience of language not only by adapting models to assess different, regionally specific levels of processing within the language processing hierarchy, but also by fine-tuning models at different levels of temporal resolution depending on the processing level within this hierarchy. Several recent ECoG studies illustrate the importance of explicitly accounting for the dynamics of the system (Dichter et al., 2016; Moses et al., 2016; Pasley et al., 2012). The challenge for future work will be to extend these approaches within the context of language neuroscience research to non-invasive, whole-brain, ideally time-resolved studies (Gwilliams & King, 2020; Loula et al., 2018). This would allow to elaborate language processing models with respect to temporal dependencies, and to reveal how these are gradually abstracted across different levels of the processing hierarchy across the brain.

In vision, a field where data-driven methods have led to more easily interpretable results than in the auditory domain, several research groups propose to use detailed hierarchical artificial neural network models to address neural information transformation processes along the visual pathways (Cichy et al., 2014; Mohsenzadeh et al., 2019). Bashivan et al. showed that images synthesized by artificial neural networks can precisely and selectively activate neural populations in specific regions of the monkey visual system (Bashivan et al., 2019). Such tools can also be used in a powerful way in the field of speech and audition, as artificial neural networks can decode, with high precision, the latent structure learned from single trials, revealing a rich, hierarchical organization of linguistic features (Livezey et al., 2019). These examples illustrate how the reverse engineering of artificial neural networks can allow to gain a deep understanding of neural processes underlying complex cognitive functions (Kell et al., 2018; Saxe et al., 2021).

Can we get rid of behaviour?

Drawing on unsupervised sorting of mouse neuronal activity, Rubin and colleagues found that neurons could be classified based on their internal tuning properties rather than on external variables such as a pre-defined stimulus (Rubin et al., 2019). The technique used by the authors, i.e., non-linear dimensionality reduction, has some definite advantages since it can reveal informative patterns of neural activity that are not tied to a particular model of the stimulus set (Zylberberg, 2018). This study suggests that one could investigate brain circuits for which little is known about the identity of the variables they

encode, in the same way that dimensionality reduction can be leveraged for probing the representational space of brain regions for which the natural dimensions of the feature space are unknown, these primarily being high-order associative regions. Whether we can truly get rid of any behavioural benchmark using multivariate pattern analyses or other machine learning methods, and whether we can elicit or modify specific behaviours by artificially inducing multivariate patterns (e.g. using stimulation techniques or brain computer interfaces (Ezzyat et al., 2017; Shibata et al., 2019)) are primordial issues for future research (Grootswagers et al., 2018; Krakauer et al., 2017; Panzeri et al., 2017).

Conclusion

With examples from the speech and language literature, we illustrate strengths and weaknesses of using machine-learning inspired methods as alternatives to classical GLM methods. The fact that machine-learning inspired methods impose little constraint on how information is selected and classified, and on how dimensions are extracted, allows to reveal unexpected structure in the data, for example in the form of multidimensional, spatially distributed representations. But this higher sensitivity to non-predicted dimensions may come at the cost of not seeing the true structure that the underlying neuronal populations represent, and hence, of missing dimensions in the data that truly relate to the observed behaviour (Carlson et al., 2017). Addressing these specific concerns may require the use of adjusted methods, which take advantage of biologically informed priors so as to functionally limit the size of the model space (Ahlheim & Love, 2018; Snoek et al., 2019).

In the era of big data, it is now commonplace to say that scientists need theory more than ever. Two decades ago, science-fiction writer Ted Chiang wrote a premonitory article in *Nature* purporting to celebrate the 25th anniversary of the last human scientific publication (Chiang, 2000). In this provocative, futuristic short-story, science is now exclusively conducted by genetically improved humans, called "metahumans", and all that remains for human scientists is the interpretation of metahuman data. "In the face of metahuman science, humans have become metascientists". It is of course tempting to see metahuman science as a metaphor for the use of artificial intelligence methods, whose inner functioning and scientific output sometimes appear to lie beyond the reach of our understanding. But data are rarely, if ever, self-explanatory. They make sense to the extent that they validate or falsify theoretically informed predictions. When it comes to interpreting data-driven findings, possessing a biologically informed theory beforehand retains some usefulness. "Human researchers", says Chiang, "may discern applications overlooked by metahumans, whose advantages tend to make them unaware of our concerns". The same surely applies to data-driven methods, whose appeal and advantages often make us oblivious to theoretical concerns.

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