Capturing cross-session neural population variability through self-supervised identification of consistent neuron ensembles

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Abstract

Decoding stimuli or behaviour from recorded neural activity is a common approach to interrogate brain function in research, and an essential part of brain-computer and brain-machine interfaces. Reliable decoding even from small neural populations is possible because high dimensional neural population activity typically occupies low dimensional manifolds that are discoverable with suitable latent variable models. Over time however, drifts in activity of individual neurons and instabilities in neural recording devices can be substantial, making stable decoding over days and weeks impractical. While this drift cannot be predicted on an individual neuron level, population level variations over consecutive recording sessions such as differing sets of neurons and varying permutations of consistent neurons in recorded data may be learnable when the underlying manifold is stable over time. Classification of consistent versus unfamiliar neurons across sessions and accounting for deviations in the order of consistent recording neurons in recording datasets over sessions of recordings may then maintain decoding performance. In this work we show that self-supervised training of a deep neural network can be used to compensate for this inter-session variability. As a result, a sequential autoencoding model can maintain state-of-the-art behaviour decoding performance for completely unseen recording sessions several days into the future. Our approach only requires a single recording session for training the model, and is a step towards reliable, recalibration-free brain computer interfaces.

1 Introduction

Neural decoders require stable neurons in a recorded population in order to accurately predict behaviour such as movement or to allow decoding of stimuli. However, over time instabilities in the recording equipment and drift in neural activity lead to instabilities that prevent re-using a decoder trained on one day for a session recorded on another day [Huber et al., 2012, Ziv et al., 2013, Driscoll et al., 2017]. At the same time, neural population activity is highly structured and often confined to low-dimensional manifolds [Cunningham and Byron, 2014] that can be recovered using latent variable modelling approaches [Hurwitz et al., 2021]. Importantly, recent work showed that movement-related latent neural dynamics in population activity from the primate motor cortex is stable and could be

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recovered over intervals as long as two years [Gallego et al., 2020]. This suggests that despite the variability at the level of single neurons, in each session a subset of neurons will remain informative about behaviour. A stable cross-session decoder therefore has to be able to identify these neurons and utilise them for decoding. Therefore we focus on identifying a maximal number of known recording neurons across unseen sessions. In this way we can decode behaviour (in our case arm movement) with high accuracy across unseen sessions by aiming to inform a decoding model of which neurons in a population are known neurons. Furthermore, we aim to inform our decoding model of which position in a seen training session dataset a given known neuron was observed at.

We achieve this neuron detection by training a recurrent neural network (RNN) to predict original neuron positions after recording data has been perturbed in a manner mirroring session to session variability. In essence, the closer our perturbations mimic real inter-session variability (as shown in Figure 1), the higher our behaviour prediction performance on an unseen session. These perturbations include adding spikes to existing neurons from randomly generated neurons, removing spikes from existing neurons, shifting the entire neuron population by a constant amount, slightly shifting neurons in time, replacing neurons with randomly generated neurons and eliminating neurons entirely.



Figure 1: Inter-session ensemble variability possible when recording from neural populations. Neurons from the original recording session can be lost to the recording array, new neurons can become visible, neurons can move between electrodes, original neurons can be replaced by unseen neurons and the entire probe array can shift, causing a systematic change in neuron position. In addition, spike sorting can induce variability as the signal to noise ratio of individual neurons changes between sessions. The perturbations we apply to each trial of recordings is in response to each of these sources of variability. We model each unseen test trial as an instance of a perturbed seen train trial and subsequently, our sequential autoencoder model attempts to map each unseen trial to a known trial.

This neuron locator RNN is trained to predict original neuron position within a single recording session from many perturbed variations of trials of this training session. Once trained to predict original neuron positions, a separate network, which in this case is a sequential autoencoder based on Latent Factor Analysis via Dynamical Systems (LFADS) [Pandarinath et al., 2017], is trained to predict original unperturbed neural recording trials from perturbed variations of trials from the same session. The encoder of this sequential autoencoder receives as input the embedding of the neuron locator RNN activations, allowing the encoder to produce latent variables which are informative enough to accurately reconstruct the original recording. The encoder produces latent variables which are also separated by behaviour (in this case arm movement direction) in a self-supervised manner, from which behaviour can be predicted without the model being explicitly trained on behaviour.

Importantly, the joint neuron locator RNN and LFADS encoder ensemble can predict behaviourally relevant latent variables for unseen sessions of recording data, with high decoding accuracy possible from these latent variables. Currently, there are no existing approaches to accurately predict behaviour from an unseen recording session when training on just one seen session. We not only show this is possible with our method, but that our approach is robust to inter-session variability for up to 8 days when a sufficient number of neurons are persistent across sessions.

2 Related Work

There have been many recent approaches to creating robust behaviour decoders of neural activity [Gallego et al., 2020, Farshchian et al., 2019, Sussillo et al., 2016, Wen et al., 2021, Karpowicz et al.,

2022, Wimalasena et al., 2021]. However these methods are not capable of decoding behaviour from a previously unseen recording session if the recorded activity is subject to random fluctuations.

Recent work in modelling neural activity shows the consequences of selectively perturbing neural data in order to learn relevant latent variables in a self-supervised way using an autoencoder [Liu et al., 2021, Azabou et al., 2021, Zhu et al., 2021]. These models take different views of the same neural data and align the latent spaces of these views once passed through an encoder, with the ultimate aim of reconstructing these views. We utilise a similar technique to train our sequential autoencoder by aligning the latent variables of perturbed versions of the same data and aim to generate the activity of the original unperturbed trial. Importantly, Liu et al. [2021] propose a model which is invariant to the specific neurons used to represent the neural state within training data; in this work we look at unseen sessions and so do not aim to produce a model invariant to new neurons, but one that is able to identify and utilise seen neurons to reconstruct unperturbed trials.

Gonschorek et al. [2021] and Jude et al. [2022] use domain adaptation to align data across recording sessions. In both, the authors use an autoencoder model and a domain classifier. However these models require training on many days of recording sessions for good behaviour decoding accuracy. Jude et al. [2022] notably requires as many as 12 training sessions and training on behaviour explicitly in order to produce high behaviour decoding accuracy on an unseen test session. In this work we achieve state-of-the-art behaviour decoding performance on an unseen test recording session while using just one training recording session, and show that this decoding accuracy can be maintained many days into the future without recalibration.

Here we train an RNN to predict original neuron position from perturbed trials and utilise this network to inform the sequential autoencoder model. This is considered self-supervised learning as we do not train our model on behaviour explicitly but instead train on the subtasks of predicting original neuron positions and reconstructing unperturbed trials from perturbed ones. This approach is analogous to that used in Noroozi and Favaro [2016], where authors form 9 subsets of images and randomly permute these subsets, then task the model with predicting the permutation. This is an example of self-supervised learning where the model is trained to understand the structure of separate classes of images and how this structure differs between classes. Here we model each trial from an unseen session of neural recording as a perturbed known trial, and aim to capture as much session to session variability as possible with the applied perturbations. Our approach produces a session invariant behaviour decoder performing with high accuracy when a sufficient number of known neurons are still present in the neuron ensemble of an unseen session.

3 M1 Recordings



Figure 2: Experimental setup: In each trial one randomly chosen target direction (indicated by one of 8 coloured circles) appears on screen, and the monkey is instructed to control the cursor (white circle) by moving the manipulandum. The monkey moves the cursor to the target location after a go cue. The collected data for each trial consists of the neural spikes and monkey hand position across all timesteps. We predict hand position from neural spikes at each timestep.

We apply our model to data from a previously published experiment [Gallego et al., 2020]. In this experiment, two monkeys were trained to perform a center-out reach task towards eight outer targets. On a go cue, each monkey moves a manipulandum along a 2D plane to guide a cursor on a screen to

the target location (Figure 2). On successful trials a liquid reward is given. Spiking activity from the motor cortex (M1) along with the 2D hand position were recorded during each trial. Spike trains were converted into spike counts in 10ms bins, and behaviour variables are used at the same resolution. In this work, only successful trials are used, all trials are aligned to movement onset and cut from movement onset to the shortest reach time across all trials.

For our analysis, we train our model on one session of recorded data from a single day which we denote day 0 (containing 173 trials for both monkeys) and test on subsequent held out days of recordings for each monkey. We expect firing patterns and neural ensembles to vary considerably more significantly the further the day of the held out recording session is from the original training session, especially as changes between consecutive days compound for days further away. In total we used 5 days of recordings for both monkeys, with 55 recorded neurons across all sessions for Monkey C and 17 for Monkey M. Each day for each monkey consists of one recording session.

4 Data Perturbations



Figure 3: Perturbations applied simultaneously to each trial of neural data, demonstrated with a simple 5 neuron system. A) Replace entire spike train with a randomly generated neuron of the same firing rate as the original neuron. B) Spikes randomly added to spike train proportional to average firing rate of all neurons in a given trial, to mirror influence of nearby newly added unknown neurons. C) Spikes randomly removed to mimic removal or movement of nearby known neurons. D) Deletion of entire neurons to simulate neuron loss between sessions, with randomly generated neurons introduced as the first or last neuron of the trial to keep neuron number consistent. E) Small random time jitter of all neuron spike trains to simulate experimental variation between sessions. F) Constant random shift of the order of all neurons to mirror probe shift.

Figure 3 outlines the perturbations forming each variation of a single trial during the training of our model. Perturbations A) to D) in Figure 3) are applied with equal probability to a given neuron of a given trial. Perturbation E) is applied to all neurons, time jitter is chosen randomly between -30ms and +30ms. Perturbation F) is applied to all trials, the amount of this neuron shift is chosen randomly between 0 and 25% of the total number of neurons. We hypothesise that this combination of transformations closely mirrors the real day to day changes of recorded neuron ensembles (Fig. 1).

5 Model

Our modelling approach is based on the hypothesis that the perturbations mentioned above can capture the substantial variability between recording sessions from the same animal. We also expect neural activity x is related to the latent variables z through a simple function, however, this function will differ between recording sessions as we expect to observe different neurons in each session. The problem is thus to find the correct encoding function z = f(x) to transform perturbed neural activity into latent variables which then allows decoding of behaviour. In addition, we require z_i for each trial i to be similar despite variations in the activity x_i .

We first train a fully connected layer and an RNN to predict original neuron position in perturbed trials. We apply the perturbations from Figure 3 to each trial, then task the network to predict the original position of each neuron in the recording data or whether it was previously unseen. As seen in Figure 4, for each neuron in the recording data we project a linear read-out layer from the RNN



Figure 4: Our model consists of a neuron locator RNN (1) combined with a sequential variational autoencoding approach (2). The neuron locator (1) is trained first to identify original neuron position (or if the neuron is randomly generated) in each trial after perturbations have been applied. Then the neuron locator's weights are frozen and its activations are given as input to the encoder of the sequential autoencoder (2). Notably, we perturb recording trials when training both the neuron locator and sequential variational autoencoder. The sequential autoencoder is tasked with reconstructing the original unperturbed recording trials. The encoder of the sequential autoencoder is then incentivised to map perturbed versions of the same trial to similar latent variables. This is accelerated by imposing an alignment loss across the latent variables of variations of the same trial. The generator RNN of the sequential autoencoder predicts original trials from latent variables produced by the encoder RNN.

which each form a probability distribution of predicted original neuron position across all possible positions (plus an extra position indicating that the neuron was randomly generated). Each of these is compared against a one hot encoding of the original neuron position before any perturbations have been applied. If the neuron is randomly generated then the one-hot encoding is one at the dedicated extra position. Predictions of original neuron position are made as follows:

$$x'_{i,1:T} = \operatorname{Perturb}(x_{i,1:T}),\tag{1}$$

$$acts_i = \operatorname{GRU}_{\theta_{pos}}(W_{pos}(x'_{i,1:T})), \tag{2}$$

$$pos_{i,n} = W_{neuron}^n(acts_i) \tag{3}$$

The predicted position for trial *i* and neuron *n* is then: $\operatorname{argmax} pos_{i,n}$

 W_{pos} and θ_{pos} are the parameters of the locator network used to predict original neuron position. W_{neuron}^n is the set of linear layers used to predict original neuron position, producing a probability distribution for each neuron which are trained together with a softmax cross entropy loss.

Once trained, the weights of this neuron locator network are frozen, and the activations of the RNN are used as input to the encoder of an LFADS-inspired sequential autoencoder. This input aids the encoder in predicting latent variables useful for generating original trials from perturbed trials.

As proposed by Pandarinath et al. [2017] we assume that the latent dynamics evolve autonomously provided a set of initial conditions z_i that are modelled as Gaussian random variables. These latent variables are produced for each trial by an encoder network consisting of bidirectional Gated Recurrent Units [Cho et al., 2014] (GRU). They are used to reconstruct the original trial-specific neural activity from the perturbed trials. A further bidirectional GRU is used as a generator for neural reconstruction of unperturbed trials from latent variables z_i . Training is based on Poisson likelihood for unperturbed neural activity reconstruction (as in [Pandarinath et al., 2017]).

The model is trained using real neural activity which corresponds to consistent behaviours (movement directions in a centre-out reach task, see above). The generative process of our model is as follows:

$$x'_{i,1:T} = \operatorname{Perturb}(x_{i,1:T}),\tag{4}$$

$$acts_i = \text{GRU}_{\theta_{pos}}(W_{pos}(x'_{i,1:T})), \tag{5}$$

$$z_i = W_{enc}(\text{GRU}_{\theta_{enc}}(x'_{i,1:T}; acts_i)), \tag{6}$$

$$g_{1:T} = \mathrm{GRU}_{\theta_{aen}}(z_i),\tag{7}$$

$$r_t = exp(W_{rate}(W_{fac}(g_t))), \tag{8}$$

$$\bar{x}_t \sim \text{Poisson}(r_t)$$
 (9)

where θ_{enc} and θ_{gen} are the parameters of the GRUs used to encode perturbed spike trains into latent variables and subsequently generate original unperturbed spike trains from the latent variables. W_{enc} , W_{fac} and W_{rate} are non-linear layers which produce latent variables, neural activity factors and generate firing rates respectively at each time step per trial.

At each training iteration the following three losses are simultaneously optimised using Adam [Kingma and Ba, 2015]:

$$L_{rec} = -\sum_{t=1}^{t} \log(\operatorname{Poisson}(x_{i,t}|r_t))$$
(10)

$$L_{kl} = D_{KL}[\text{GRU}_{\theta_{enc}}(z_i|x_i')||\mathcal{N}(0,I)] = -\frac{1}{2}[\log(z_{i,\sigma}^2) - z_{i,\mu}^2 - z_{i,\sigma}^2 + 1]$$
(11)

$$L_{align} = \frac{1}{P} \sum_{j=1}^{P} \sum_{k\neq j}^{P} (z_{i,j} - z_{i,k})^2$$
(12)

 L_{rec} is minimised by the encoder network and the neural generator network. As in Liu et al. [2021], we apply an alignment loss (L_{align}) across latent variables produced from perturbed trials (where P is the number of perturbations of a given trial) of the same original trial z_i which reduces training duration. We form 2 perturbed variations of each trial in a given batch at each training iteration. Kullback–Leibler (L_{kl}) divergence loss (between a multivariate standard Gaussian distribution and the encoder-generated latent variables) and L_{align} are minimised by just the encoder network. Thus the total error for all parameters in the model across all training trials can be summarised as:

$$E(\theta_{enc}, W_{enc}, \theta_{dec}, W_{fac}, W_{rate}) = \frac{1}{N} \sum_{i=1..N}^{i} L^{i}_{align}(\theta_{enc}, W_{enc}) + L^{i}_{rec}(\theta_{enc}, W_{enc}, \theta_{gen}, W_{fac}, W_{rate}) + \lambda_{kl} L^{i}_{kl}(\theta_{enc}, W_{enc})$$
(13)

 λ_{kl} is the weight of Kullback–Leibler (KL) divergence which rises exponentially as training progresses. We name our model CAPTure and Identify Variability at Target Ensembles (CAPTIVATE). Further implementation details can be found in Appendix A.

5.1 Comparison models

We compare the ability of CAPTIVATE to predict behaviour from sessions of unseen spike data against existing methods and against a variation of our own model where we do not use the locator network trained on original neuron position to aid in aligning perturbed trials. We denote this model variation CAPTIVATE-noLoc. In addition, we look at vanilla LFADS [Pandarinath et al., 2017] in autoencoding trials without any perturbations. We also compare against a baseline RNN (GRU) with a linear readout layer explicitly trained to reconstruct movement behaviour from neural activity.

For all autoencoding models we use a separately trained GRU network to predict behaviour from the latent space of these models. We do not include ADAN [Farshchian et al., 2019], NoMAD [Karpowicz et al., 2022] or the generative model by Wen et al. [2021] as all require at least some training data from a held out session or subject to be effective. We also do not test against Gonschorek et al. [2021] or [Jude et al., 2022] as these approaches require many training sessions to be effective in predicting behaviour from an unseen session whereas we aim to do this with just one training session.

6 Results

Figure 5 shows behaviour decoding performance of CAPTIVATE for an unseen session that was recorded the day after the training session for different total rates of perturbation. A total perturbation rate of 40% (i.e a rate of 10% for each perturbation A) - D) in section 4) for both monkeys appears to be optimal. At perturbation rates above 40%, neural activity from perturbed day 0 train trials with a particular target movement direction begin to resemble original trials of other movement directions, and thus hurt alignment. Perturbation rates below 40%, particularly for Monkey C, are not sufficient to simulate the inter-session variability between day 0 and day 1 recordings. Training the neuron locator RNN on a total perturbation rate of 40% for both monkeys yields 85% and 93% accuracy on predicting original neuron position from perturbed trials from Monkey C and Monkey M respectively on their day 0 train session.



Figure 5: Behaviour decoding performance on an immediately subsequent unseen session (day 1) of CAPTIVATE at different rates of total perturbation. Total perturbation rate is the sum of the rates of perturbations A) - D) outlined in section 4, each of which are applied at equal rates.

Using the optimal rate of 40% of perturbation to trials from both monkeys when training CAPTIVATE leads to the results seen in Figure 6. For both monkeys we see high behaviour decoding performance on the unseen session from day 1, surpassing previous methods. CAPTIVATE maintains high behaviour decoding performance for Monkey C on an unseen session up to 8 days after the day 0 training session was recorded. Notably, behaviour decoding for Monkey C is much more stable for future unseen sessions than for Monkey M. This is likely due to recording sessions from Monkey C containing more than 3 times as many neurons as Monkey M.



Figure 6: Behaviour prediction performance when testing all models on completely unseen recording sessions. We report the mean R-squared between the inferred and true x,y positions. Each model is tested on unseen sessions from an increasing number of days into the future from the original training session (day 0) for both monkeys. Each day 0 train session is run 10 times with different random seeds, with error bars showing standard deviation when applied to each unseen session.

Notably in the case of Monkey M, day 1 decoding performance is high at all levels of perturbation from 0.1 to 0.4 (Figure 5), therefore it is likely that the session to session variability between day 0 and day 1 is small. Thus, for a subject with fewer neurons in recorded data, CAPTIVATE may only require a low rate of total perturbation when aligning nearby unseen sessions.

CAPTIVATE-noLoc, Vanilla LFADS or an RNN model cannot capture session-to-session variability even for the day 1 unseen session, as shown in Figure 7. CAPTIVATE-noLoc cannot accurately reconstruct original trials from perturbed variations of the day 0 train session, but has a similar day 0 and day 1 session behaviour decoding accuracy, implying our perturbations closely mirror intersession variability. This indicates that poor performance of CAPTIVATE-noLoc on both monkeys is due to the inability of the encoder of this model to recognise known neurons and thus, shows how crucial the neuron locator network is in recognising known neuron ensembles in unseen recordings.

LFADS is trained solely on unperturbed trials and so cannot recognise the shifts that occur between sessions as variations of the day 0 training session, but instead sees the neurons of these sessions as completely unseen, even though many of these neuron ensembles are still present across sessions. The RNN model is also trained on unperturbed trials and is even less robust to later unseen sessions than LFADS, however, this RNN baseline can recognise some behaviour in both monkeys for the day 1 unseen session, indicating a relatively low level of variability in adjacent day recordings.



Figure 7: For each monkey, *Top row*: t-SNE embeddings of latent space for CAPTIVATE when applied to each unseen session. In each embedding, points denoted by a circle are trials from the day 0 training session. Points denoted by a triangle are trials from the named unseen session. Each colour represents a target direction for the centre-out reach task. *Bottom row*: Predicted 2D monkey hand position of trials using a separately trained RNN decoder trained on the latent space of CAPTIVATE when applied to each unseen session.

Figure 7 shows t-SNE visualisations of the latent space in addition to behaviour predictions made from the latent space of CAPTIVATE when trained on unseen sessions from both monkeys. For Monkey C, this shows that the majority of trials from all unseen sessions are correctly aligned with the corresponding trials in the training data set (Figure 7, compare dots and triangles in the t-SNE plots where colour indicates movement direction; note that the latent space is well partitioned by behaviour

although the model is only trained on neural activity). Occurrences where the unseen trials correctly overlap known train trials, in turn, yields correctly decoded behaviour. The alignment becomes progressively worse for later sessions, and as the alignment is less precise, behaviour predictions also become worse. In contrast, for Monkey M the alignment of trials beyond day 2 becomes increasingly worse, a direct consequence of the smaller number of neurons in the recording.

Table 1: Mean decoding performance effects of ablating individual perturbations when training on day 0 session and tested on immediately subsequent (day 1) unseen session for both monkeys.

Ablation	No-Replace	No-Add	No-Remove	No-Delete	No-Jitter	No-Reorder
C Mean R^2	0.66	0.79	0.74	0.49	0.77	0.70
M Mean R^2	0.71	0.75	0.81	0.63	0.81	0.77

Ablations of individual perturbations (as outlined in Figure 3) applied when training on the day 0 session reveal that perturbations which introduce randomly generated neurons and alter the continuous ordering of neurons have the highest impact on unseen session behaviour decoding performance. This analysis is summarised in Table 1 and shows that neuron deletions, replacements and probe shifts cause the majority of inter-session neuron ensemble variability. Nonetheless, a combination of all perturbations are necessary for the decoding performance achieved by CAPTIVATE in Figure 6. We also train CAPTIVATE without the alignment loss in Eq. 12, which produces a behaviour decoding mean R-squared of 0.82 on Monkey C and 0.85 on Monkey M on trials from the day 1 unseen session. This minimal drop in decoding performance when training without an explicit alignment loss is consistent with results from [Liu et al., 2021].

7 Discussion

In this paper we use a self-supervised approach, CAPTIVATE, to train a model to recognise and correct for session-to-session variability in neural recordings. We then show that the combination of this model with a latent variable model that identifies low-dimensional dynamics in neural activity yields a model that is now robust variability between recordings sessions. The model is capable of successfully predicting behaviour with high accuracy from unseen sessions, surpassing previous work by Jude et al. [2022] when comparing against subsequent day decoding performance. Furthermore, our approach leads to relatively high and stable behaviour decoding performance on unseen sessions many days into the future when a sufficient number of neurons are persistent across sessions. As a result, this method performs better for data sets with more recorded neurons (Monkey C), while for fewer neurons the performance degrades more quickly, only producing good results for sessions close in time to the training session (Monkey M).

CAPTIVATE may prove significant when applied to Brain-Computer Interface (BCI) systems, as it reduces the need to frequently recalibrate a behaviour decoder. Moreover, our model is fast and inexpensive to train, as just one session of recordings is required to provide stable decoding for many subsequent days. This places modest requirements on hardware, a single GPU is sufficient, and inference is fast and can be performed in real-time. CAPTIVATE uses neural data alone to produce latent variables which are separated by behaviour in a self-supervised way, therefore behaviour recording is not explicitly required to train the model. In BCI applications, unsupervised methods could generate behaviour from the latent variables, reducing the resources required for these interfaces.

With CAPTIVATE we achieve stable behaviour decoding performance for up to 8 days, which is followed by a slow decline in performance. The decline is due to an increase in variability that could no longer be compensated. This would require a model to correct even stronger perturbations, but training a model this way leads to an overall decrease in performance even for short time intervals (Figure 5). Therefore long-term stable decoding currently still requires re-training of the components of a latent variable encoder model such that the altered neural dynamics are re-aligned with the latent dynamics [Wen et al., 2021, Karpowicz et al., 2022, Farshchian et al., 2019]. Equally, our model fails to successfully decode behaviour from recordings from an unseen animal as this requires a more complex mapping function between activity and latent space [Wen et al., 2021].

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