Neural Manifolds

LETTER

doi:10.1038/nature13665

Neural constraints on learning

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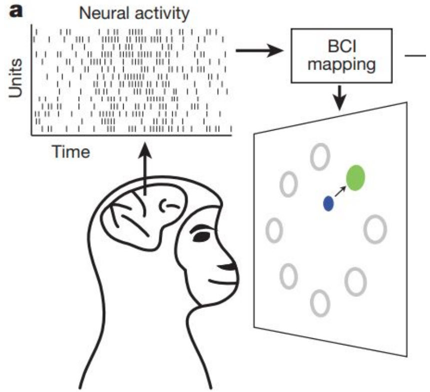
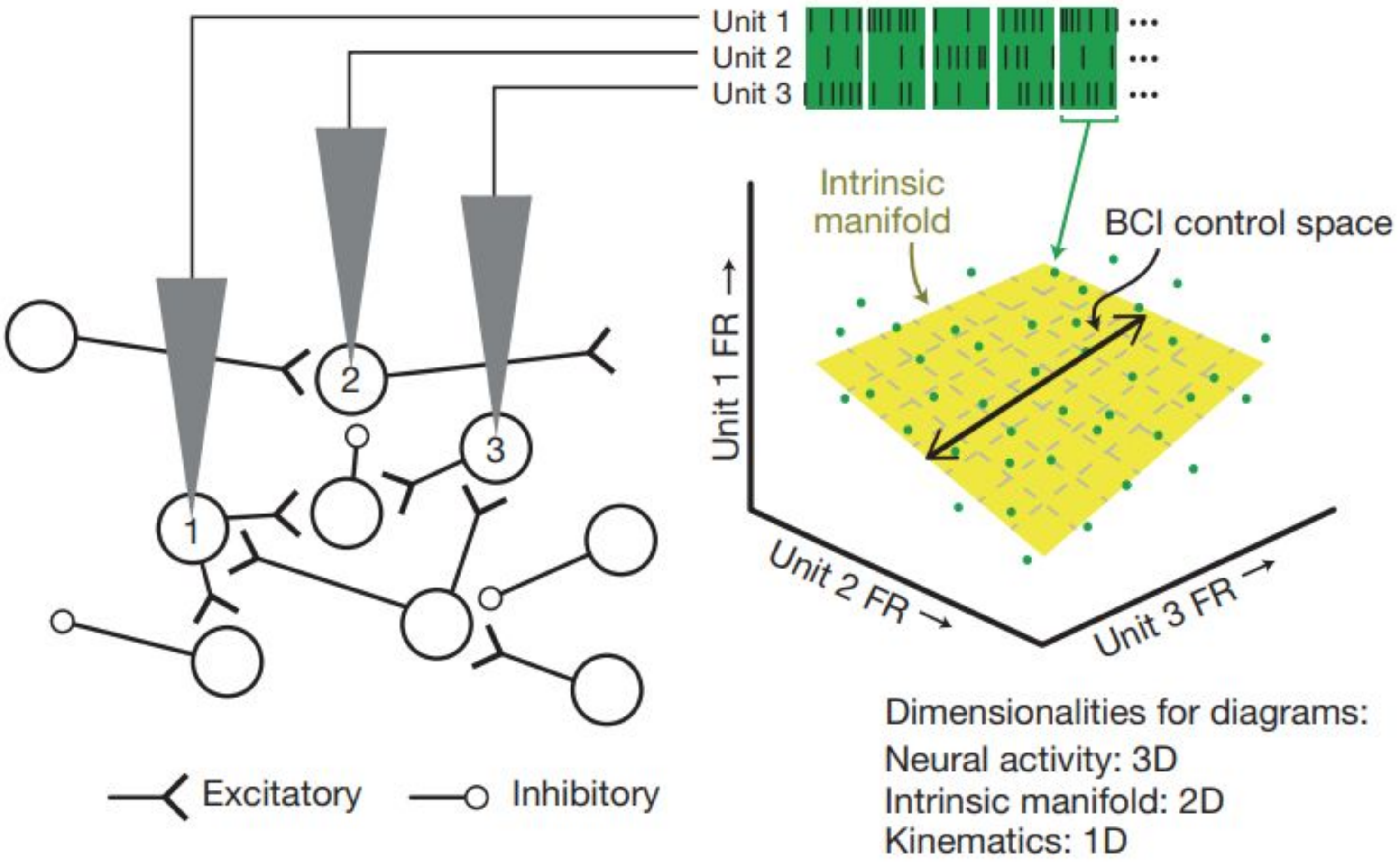
Hypothesis and Setup

- Hypothesis - ease or difficulty with which an animal can learn a new behaviour is determined by the properties of the corresponding neuron network
- Tested on BCI paradigm - since all relevant neurons can be monitored
- BCI Task: Move a cursor to circles on screen using only neural activity



Terminology

- **Neural Space** - each axis corresponds to activity of one neuron
- Neurons fire in relation to other neurons (could be excitatory or inhibitory relations), in other words: they **co-modulate**.
- Co-modulations imply that neural activity patterns for a task does not span entire neural space - only a subspace called the **intrinsic manifold** (which needs to be identified)
- The **control space** or the BCI mapping is the subspace within the intrinsic manifold that is responsible for the neural patterns that relate to the velocity of the cursor (task output in 2 dimensions)



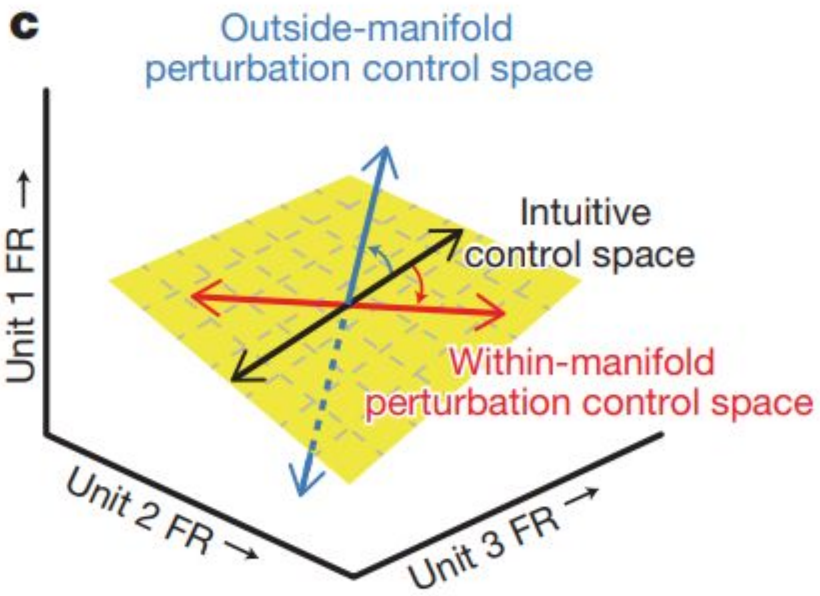
Unit 1
Unit 2
Unit 3
Intrinsic manifold
BCI control space
Unit 1 FR →
Unit 2 FR →
Unit 3 FR →
1
2
3
Excitatory
Inhibitory
Dimensionalities for diagrams:
Neural activity: 3D
Intrinsic manifold: 2D
Kinematics: 1D

Experimental Manipulation

Objective was to alter the control space and reposition it either within or outside the intrinsic manifold

1. **Within-manifold Perturbation:** re-orienting the control space but it is kept within manifold
    a. Preserved co-modulation patterns
    b. Altered how co-modulation patterns affected cursor kinematics
2. **Outside-manifold Perturbation:** re-orienting the control space and allowing it to leave manifold
    a. Altered co-modulation patterns
    b. Preserved how co-modulation patterns affected cursor kinematics

c

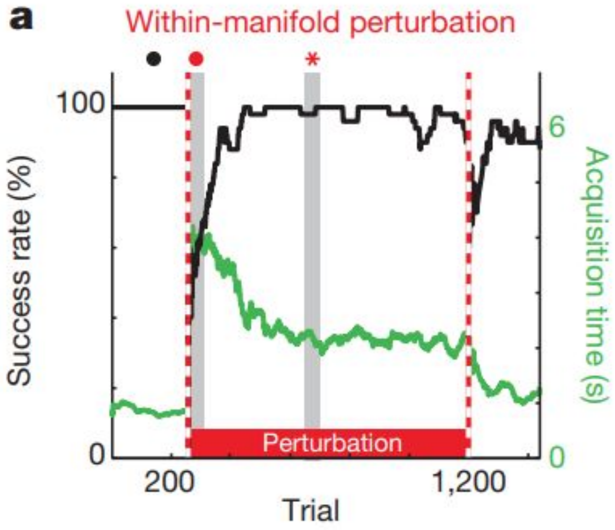


Outside-manifold
perturbation control space
Intuitive
control space
Within-manifold
perturbation control space
Unit 1 FR →
Unit 2 FR →
Unit 3 FR →

Hypothesis with the new terminology

- In both type of perturbations, monkeys suffered impaired performance on task and the experimenters observed whether they regained proficient cursor control
- Done by learning new associations between natural co-modulation patterns
- After an outside-manifold perturbation, monkeys had to **generate new co-modulation patterns** within the recorded neurons
- Updated hypothesis: Within-manifold perturbations are easier to bounce back from (by relearning) than outside-manifold perturbations

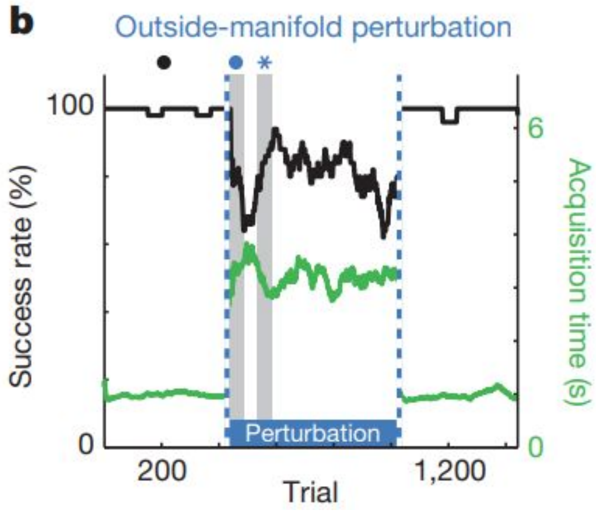
Within-manifold Results



- Performance improved over time after exposure to perturbation - learning did occur

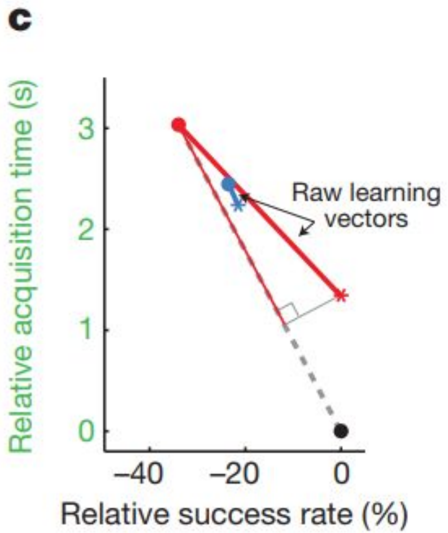
(dashed lines indicate BCI mapping changes - introduction and removal of perturbation)

Outside-manifold Results



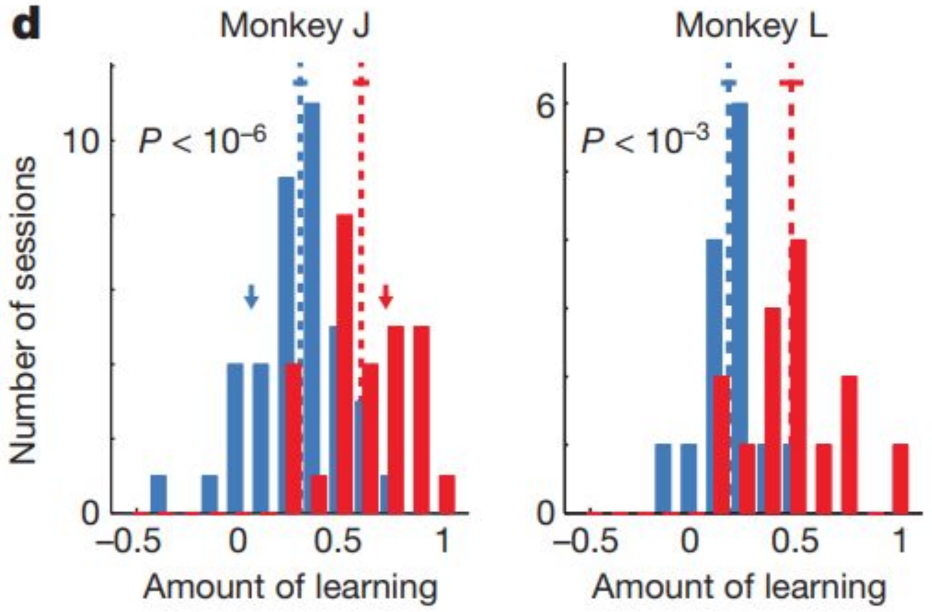
- Performance did not really improve over time after exposure to perturbation - learning did not occur
- Also evidenced by **lack of impairment** after perturbation was removed (intuitive mapping restored). Different from WM.

Raw Learning - length of the vectors



Red Line - shows difference between initial performance and best performance after WM Perturbation
Blue Line - shows difference between initial performance and best performance after OM Perturbation

Amount of Learning



- BCI Performance remained impaired for OM (blue) whereas it was regained for WM (red).

Implications

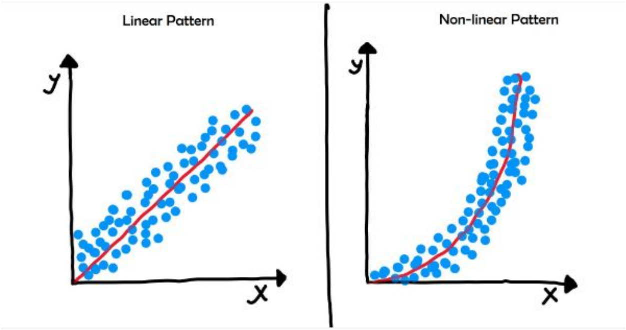
- Supports hypothesis that structure of network determines which neural activity patterns (and output behaviours) a subject can readily learn to generate
- IM is a **reliable predictor of learnability of a BCI mapping -** mappings out of manifold was harder to learn than inside
- WM uses fast-timescale learning mechanisms (adaptation)
- OM uses neural mechanisms for skill training
- Low dimensional projections of data are not just for visualisation but reveal causal constraints on behaviour
- Population patterns are more ‘controlling’ than individual neurons

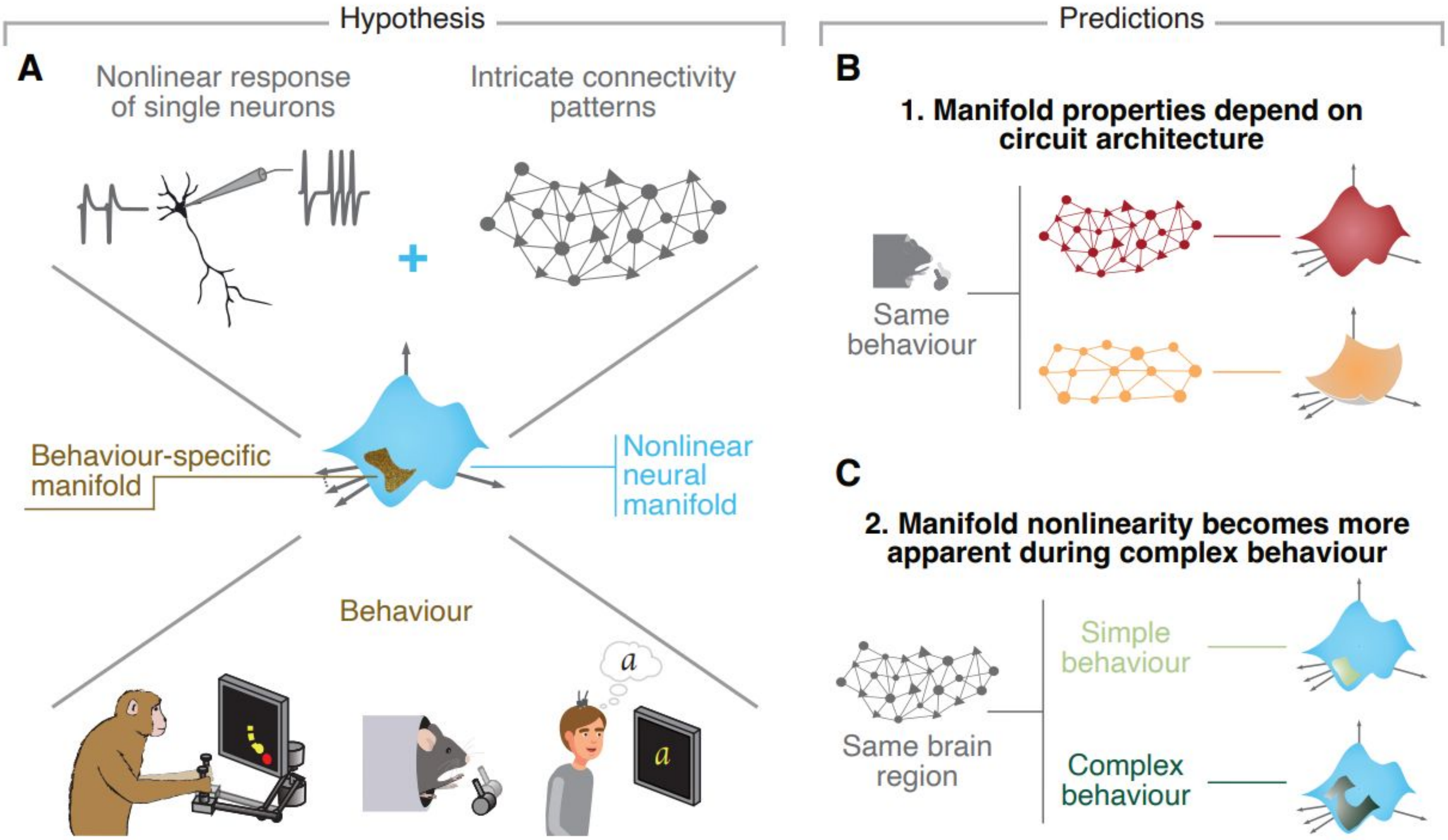
Nonlinear manifolds underlie neural population activity during behaviour

Cátia Fortunato[1], Jorge Bennasar-Vázquez[1], Junchol Park[2], Joanna C. Chang[1], Lee E. Miller[3,4,5], Joshua T. Dudman[2], Matthew G. Perich[6,7], Juan A. Gallego [1,†]

Terminology and Background

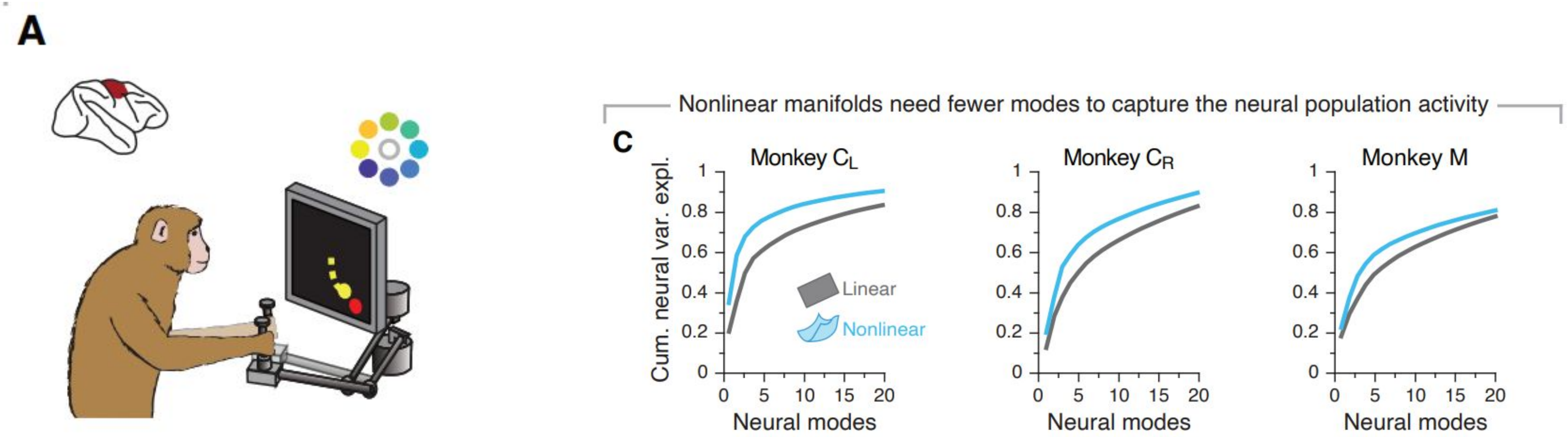
- Neural Modes - the covariation (comodulation) patterns of a population of neurons within a given brain region
  - These give rise to the ‘manifold’
  - They are treated as ‘dimensions’ in this study
- Neuron activity is nonlinear - a firing threshold is required to generate AP
- Neurons are also connected in a very complex manner
- If the neuron itself is nonlinear and if its interaction with other neurons are complex and likely nonlinear - **shouldn’t the resultant manifold also be similarly nonlinear?**




Hypothesis
Predictions
A
Nonlinear response of single neurons
Intricate connectivity patterns
Behaviour-specific manifold
Nonlinear neural manifold
Behaviour
a
a
B
1. Manifold properties depend on circuit architecture
Same behaviour
C
2. Manifold nonlinearity becomes more apparent during complex behaviour
Same brain region
Simple behaviour
Complex behaviour

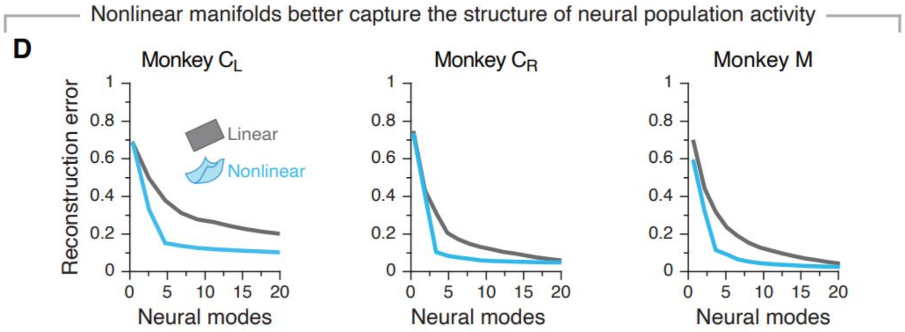
Result 1 - Motor cortical manifolds are nonlinear

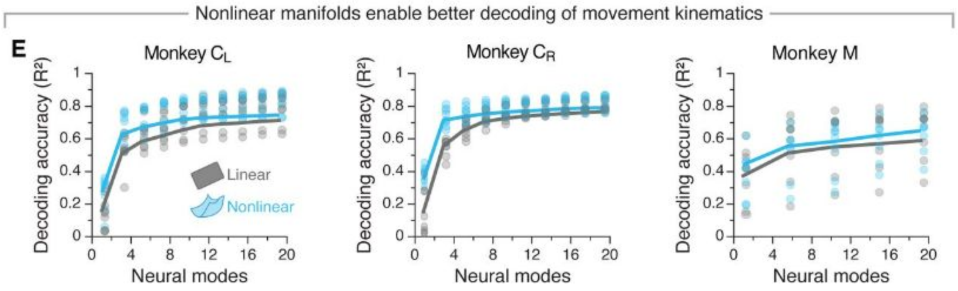
- Monkey motor reaching experiment set up and neural recordings
- PCA used to identify flat manifolds underlying data
- Isomap used to identify nonlinear manifolds underlying data
- Isomap is a better 'model fit' - more variance explained with fewer modes



Additional analyses

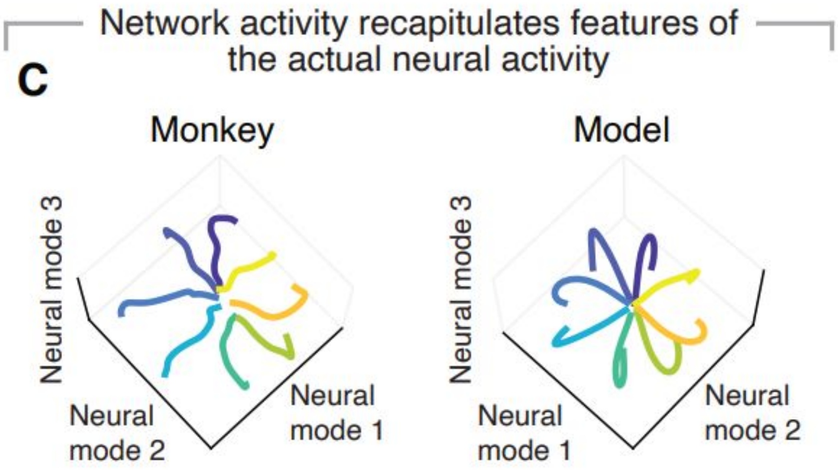
- Reconstruction error - how well can these latent dynamics used to reconstruct the full dimensional activity
- Nonlinear manifolds had lower reconstruction error at lower dimensions
- Linear decoders trained on the dynamics within nonlinear manifolds performed better than those trained on linear manifolds





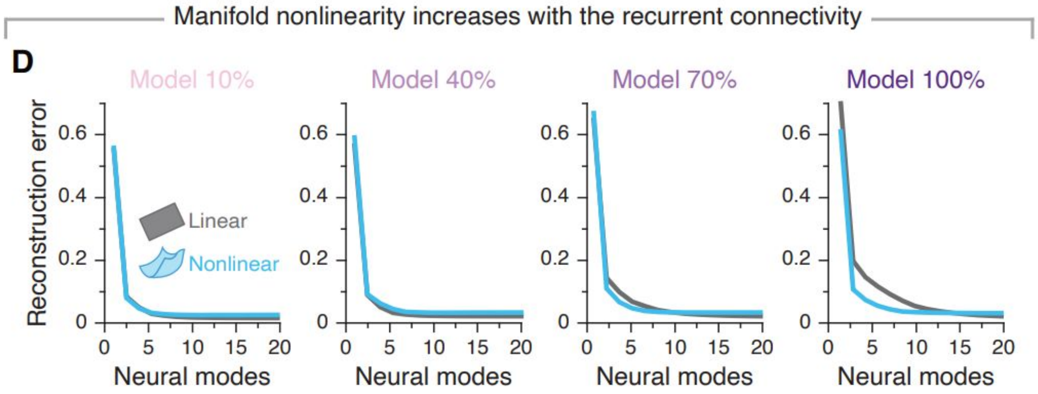
Results 2 - Emergence of nonlinearity from circuitry

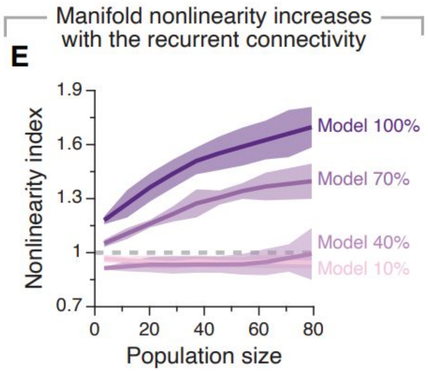
- Same task but with RNNs - they output hand velocity during each trial and used preparatory neural activity as input
- RNNs were able to perform well and simulate the neural output of monkeys to a sufficient degree



Results 2

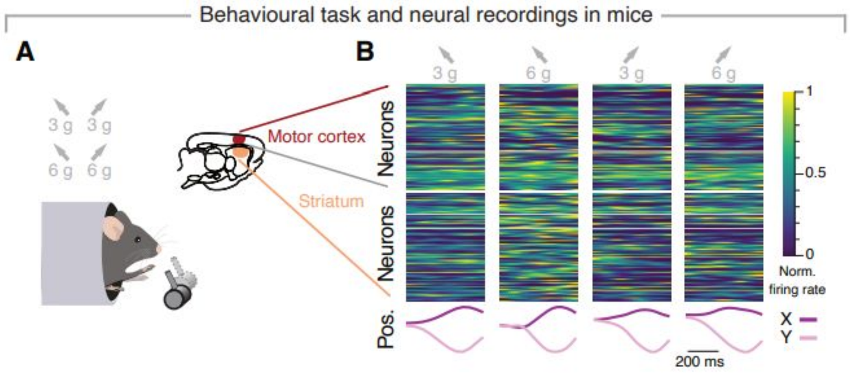
- Investigation between degree of recurrent connectivity and manifold nonlinearity
- More recurrence in networks - the ‘more nonlinear’ the manifolds
- Nonlinearity index - ratio between the estimated dimensionality of linear and nonlinear manifolds for same number of neurons
- Manifold nonlinearity increases with level of recurrence in networks





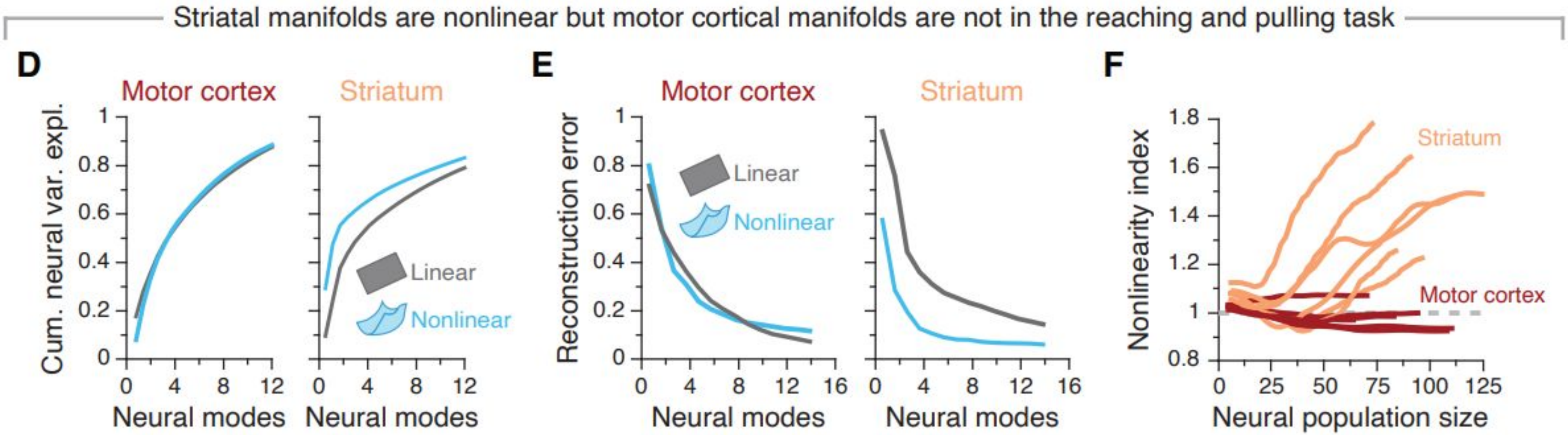
Result 3 - Nonlinearity changing across brain regions

- Follows from second result that different connectivity patterns lead to different degrees of nonlinearity
- Similar reaching task where mouse Motor Cortex and Dorsolateral Striatum neural activity was recorded
- Motor cortex has more cellular nonlinearities than the striatum - better modelled by a nonlinear manifold?



Result 3

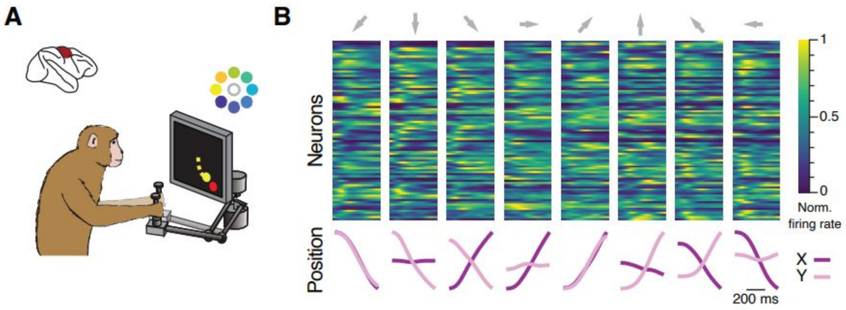
- No:

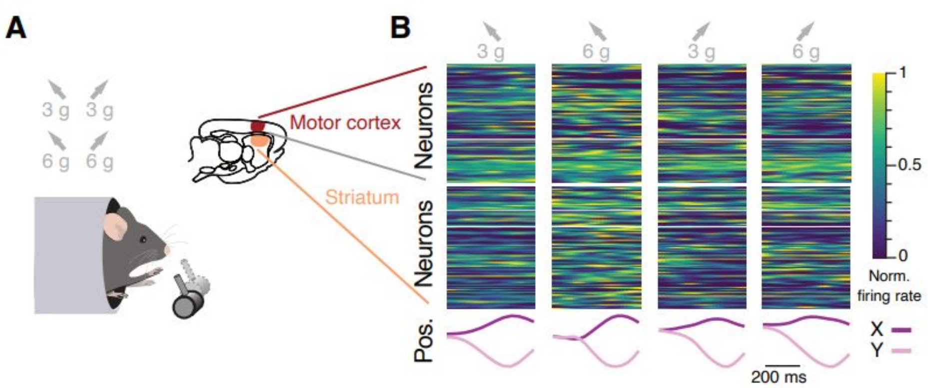


- Striking differences in nonlinearity - motor cortex flatter than striatum
- Circuit properties may be the primary factor underlying neural manifold nonlinearity rather than individual neuron nonlinearities

Result 4 - Task Complexity

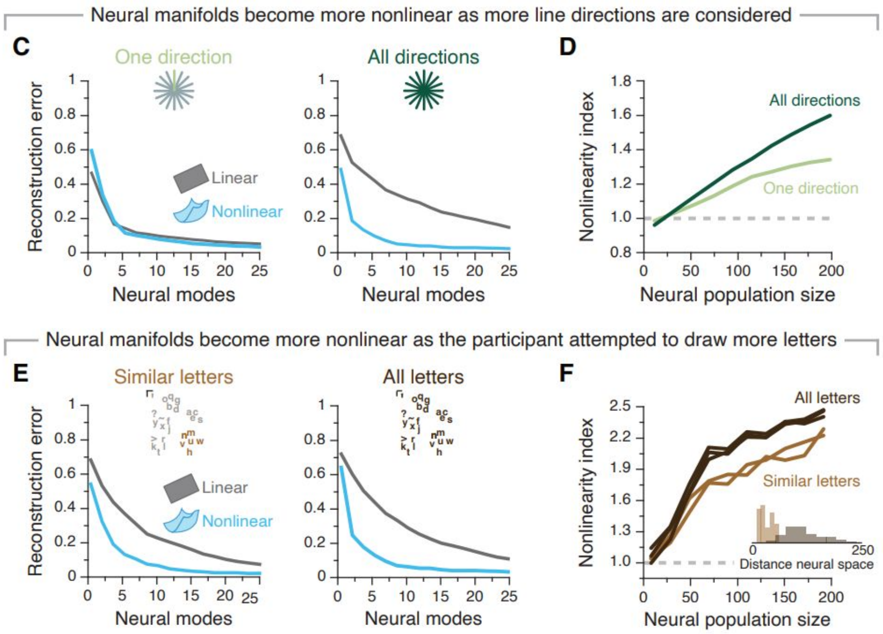
- Interesting contrast - monkey motor cortex manifolds were nonlinear whereas mouse motor cortex manifolds were flat
- Monkey reaching task was more complex - required a wider variety of muscle activity patterns
- Mice had it easier - only had to reach one of two positions away from body





Result 4

- Analysis of neural activity of motor cortex of a paralysed patients attempting to draw lines and letters



Takeaways

- Better suited to estimated underlying structures and patterns in neural data
- Clear evidence of nonlinear manifolds in motor regions
- Key to develop BCIs to restore function by decoding control signals?

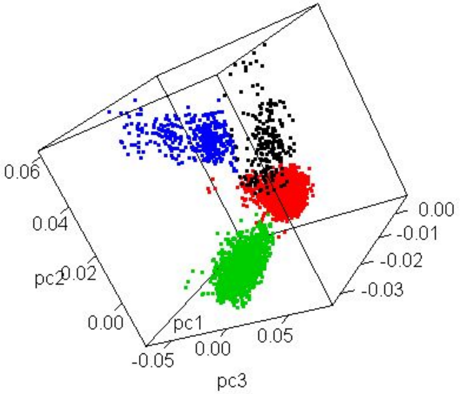
Manifold Identification

Manifold Identification

- Collect neural data for a certain task from a certain region
- Perform dimensionality reduction on the larger neural space
- If we are able to obtain a lower dimensional structure where most (or all) the ‘variance’ of the neural data lies, we can identify it as the manifold
- PCA, Isomap, LLE for dimensionality reduction

Principal Component Analysis

- PCA is a linear dimensionality reduction technique
- Identifies set of orthogonal eigenvectors as the Principal Components that captures the ‘greatest variance in the data’
- PCs are ranked based on this variance
- Manifold Learning is a generalisation of PCA - we are looking for a lower dimensional manifold (constructed by PCs)

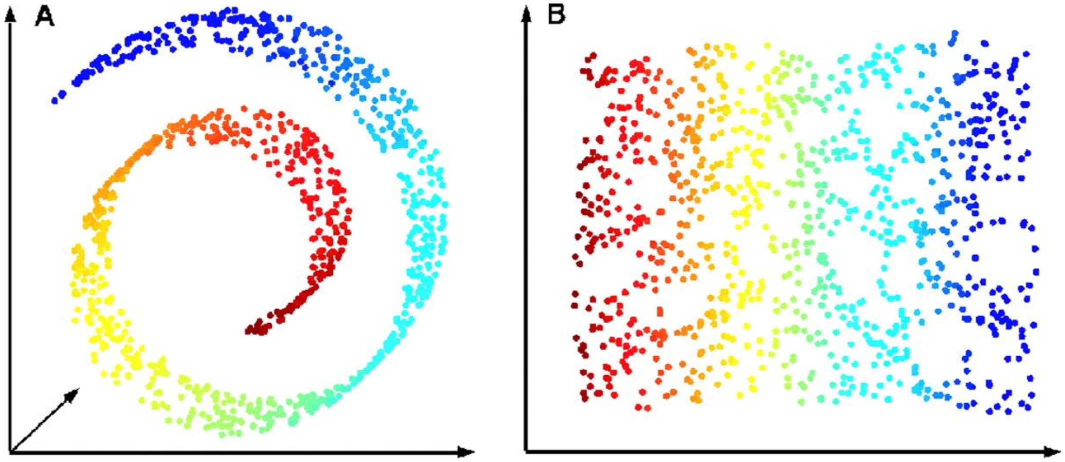


Isomap

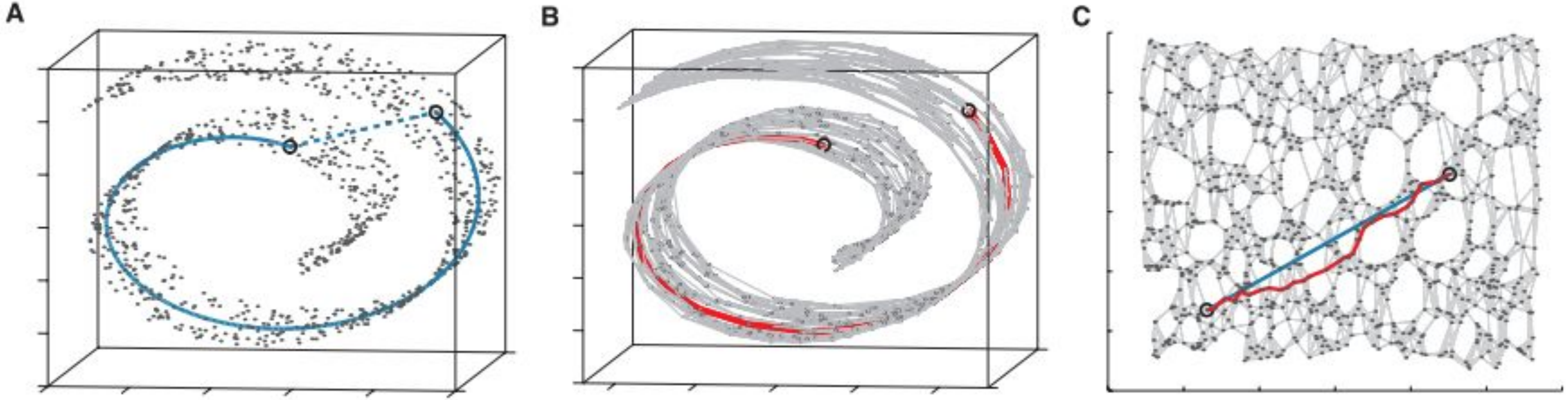
A Global Geometric Framework for Nonlinear Dimensionality Reduction

Joshua B. Tenenbaum,[1*] Vin de Silva,[2] John C. Langford[3]

- Underlying manifolds may not always be linear - how do we approximate these nonlinear manifolds?



Isomap



- Generic Euclidean Distance between points doesn’t work here
- Geodesic Distance captures the true underlying geometry of the manifold (even in a low dimensional space)
- Resulting low dimensional space where these distances are preserved

Isomap

Table 1. The Isomap algorithm takes as input the distances $d_X(i,j)$ between all pairs i,j from N data points in the high-dimensional input space X, measured either in the standard Euclidean metric (as in Fig. 1A) or in some domain-specific metric (as in Fig. 1B). The algorithm outputs coordinate vectors $\mathbf{y}_i$ in a d-dimensional Euclidean space Y that (according to Eq. 1) best represent the intrinsic geometry of the data. The only free parameter (ϵ or K) appears in Step 1.

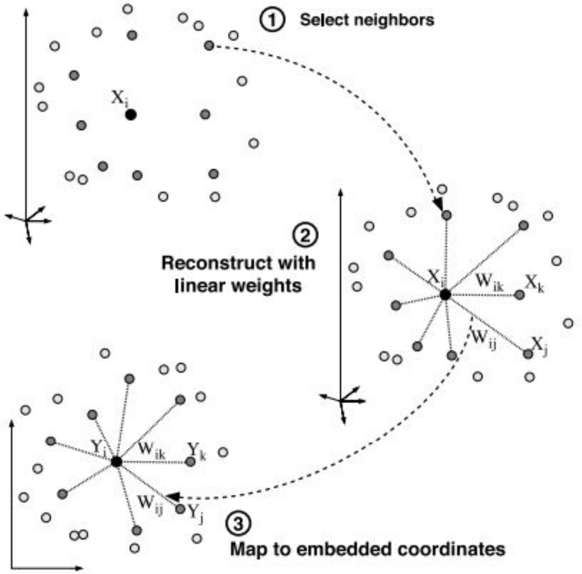
Step		
1	Construct neighborhood graph	Define the graph G over all data points by connecting points i and j if [as measured by $d_X(i,j)$] they are closer than ϵ (ϵ-Isomap), or if i is one of the K nearest neighbors of j (K-Isomap). Set edge lengths equal to $d_X(i,j)$.
2	Compute shortest paths	Initialize $d_G(i,j) = d_X(i,j)$ if i,j are linked by an edge; $d_G(i,j) = \infty$ otherwise. Then for each value of $k = 1, 2, \ldots, N$ in turn, replace all entries $d_G(i,j)$ by $\min\{d_G(i,j), d_G(i,k) + d_G(k,j)\}$. The matrix of final values $D_G = \{d_G(i,j)\}$ will contain the shortest path distances between all pairs of points in G (*16, 19*).
3	Construct d-dimensional embedding	Let λ_p be the p-th eigenvalue (in decreasing order) of the matrix $\tau(D_G)$ (*17*), and v_p^i be the i-th component of the p-th eigenvector. Then set the p-th component of the d-dimensional coordinate vector $\mathbf{y}_i$ equal to $\sqrt{\lambda_p} v_p^i$.

Locally Linear Embedding

Nonlinear Dimensionality Reduction by Locally Linear Embedding

Sam T. Roweis[1] and Lawrence K. Saul[2]

- Same motivation as Isomap
- Basic Idea - take advantage of local geometry and stitch it together to preserve global geometry on lower dimensional space



Final thoughts

- Neural activation patterns are underlied by a manifold - the subspace of the neural space that represent common activity
- ‘Learning’ takes place more readily if new demands are within manifold
- These manifolds may be better identified by non-linear dimensionality reduction techniques dependent on factors like task complexity, network properties, etc.
- Implications on Brain-Similar Nets?