In search of real dynamical behavior of neural circuits

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Discovery and implication of dynamical circuit activity

The analysis method proposed by Elsayed and Cunningham (1) aims to solve one class of problems: provide a suitable null distribution for neuron population activity. The advent of new population recording methods has allowed us to discern structures in the aggregate activity of a neural circuit that represent external input or internal state. The question arises, however, as to whether such structure is an expected result of primary features of neuron responses, such as a simple summation of their individual tuning properties. One of the more prominent results under this question is the rotation structure of motor cortex coding of reach (2). A modified bootstrapping strategy was developed to answer this question.

A traditional bootstrapping method randomly samples (with replacement) the activity of individual neurons to destroy its temporal structure and form a null distribution (3). Additional tricks were sometimes applied to bootstrapping, such as sampling small segments of neuron activity instead of single time points, to preserve some temporal smoothness in the resampled distribution. Sometimes bootstrapping was not done at sample level, but hierarchically at neuron, condition, or individual levels (4). Resampling at larger granularity keeps the temporal or inter-neuronal structure, while keeping potential information represented by firing pattern in the random sample. With simple resampling methods, it was not possible to discriminate between correlation structure in time, inter-neuron or between conditions, and emergent dynamical behaviors that are above these "primary structures".

Neuron activity in dynamical systems

Although all evolving systems are in sense dynamical systems, a dynamical system as often referred in neuroscience is one where the evolution of internal state drives the output, and external input (stimulus or control signal) indirectly changes the output by perturbing the internal state evolution (5). The evolution of dynamical systems can be described as the motion of a point in its state space. Neural circuits can have different types of dynamics, including periodic, quasi-periodic and chaotic, depending on whether this motion has one orbit, multiple orbits, or no orbits (6). A quasi-periodic system allows multiple semi-stable states and a chaotic system allows cascading response/high sensitivity to input (6). A neuron circuit being dynamical implies it being able to hold a semi-stationary state, in contrast with models in which a brain area passively responds to stimuli or generates activity patterns that match desired motor output one-to-one.

The two differentially squeezing approaches

The study proposed two methods for preserving the primary features in neuron activity while exposing interesting higher order features. The main contribution of this paper was to formalize the notion of primary features of a neural population (7). Essentially, the primary features of population activity were defined as signal statistics at 3 levels: tuning of single neurons, temporal correlation of firing rates, and signal correlations across neurons (1). These 3 levels correspond to correlation structures on the 3 margins of the population activity tensor: temporal, inter-

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neuronal, and between conditions.

Two modified bootstrapping strategies can be used to fix these 3 structures. The first one shuffles the recorded data independently for conditions and time, then applies a weight matrix to the randomized data. The weight matrix was optimized to minimize the difference between the marginal covariance matrices of the randomized data and the real data. The second method calculates the lowest entropy distribution of random data preserving the 3 marginal covariance matrices, then samples from this distribution. The second method is more computational intensive, but preserves the exact amount of correlation structure, while the first one is cheaper but may carry extra information into the null distribution (1).

With these methods, the null distribution can be calculated for new datasets, and statical tests can be performed against the null distribution to reveal any structure beyond the marginal correlations. A true population structure not arising from the temporal and spatial correlation of the neurons' activity implies unknown circuit structure or dynamics, which should lead to interesting future discoveries.

Dynamical activity can be captured in correlations

While the emphasis of these two tests are on novel emergent properties of population dynamics, there exists a gap between what they test and the original idea of dynamical neural circuits. For example, the dynamic activity reported in Churchland *et al.* (2) was indicated by persistent rotation of population data projected on primary components. Similar findings include animal decision coded in different rotations patterns in population firing in the pre-frontal cortex (8).

Both systems have often been called "dynamic" and can be roughly imagined as circuits with oscillatory activity or moving waves. In such a circuit, a subpopulation of neurons drives the increase of activity of another subpopulation while suppressing themselves. The direction of the drive depends on top-down command, and generates a rotation in the state space. This relation between neuron subpopulations, despite being an emergent population property not tied to any individual neurons' tuning properties, is partially captured by the inter-neuronal correlation structure. This tight relation between the rotation dynamic and the correlation structure is reflected in the existence of rotation structure in the null control shown in supplementary Figure 10 of the paper (1). Certain features in the original data are not captured by this null control, as evident from the statistical test performed by the authors and intuitively from the stronger attractor from the original data compared to the null control. However, the basic dynamical characteristic of system was captured in the null, as the dynamical generator model of the motor cortex activity (2) showed as much similarity to the original data as to the null with all 3 correlation structures.

The real applications

Perhaps the larger contribution of this method lies in its ability to decompose population activity structures. Since the null distribution can be constructed using an arbitrary combination of conditional, neuronal, and temporal correlation structures, it allows us to attribute a given population phenomenon to one or more of these structures. A typical oscillatory population with external perturbation would yield population activity dependent on the neuronal correlation structure. An area with dense population coding for the external input, such as early visual areas responding to naturalistic inputs, will show a structure in its response that is dependent on the structure of input, such as the temporal correlation structure in natural movies (9), or inherent biases in natural scenes. As such, the rotation structure in motor cortex coding (2) can be understood as having large contributions from inter-neuronal and inter-conditional correlations, which in no ways detract from its significance as a hallmark of a dynamical system. The coding structure for reach in the motor cortex has significant components beyond what can be captured by the marginal correlation structures, from perhaps yet unmodeled reasons. The continued effort from the authors (1,2) thus elucidate the basic dynamical coding in the cortex, and reveals novel emergent population behaviors worthy of future discoveries.

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