

The dynamics and geometry of choice in the premotor cortex

<https://doi.org/10.1038/s41586-025-09199-1>

Received: 25 July 2023

Accepted: 27 May 2025

Published online: 25 June 2025

Open access

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The brain represents sensory variables in the coordinated activity of neural populations, in which tuning curves of single neurons define the geometry of the population code^{1,2}. Whether the same coding principle holds for dynamic cognitive variables remains unknown because internal cognitive processes unfold with a unique time course on single trials observed only in the irregular spiking of heterogeneous neural populations^{3–8}. Here we show the existence of such a population code for the dynamics of choice formation in the primate premotor cortex. We developed an approach to simultaneously infer population dynamics and tuning functions of single neurons to the population state. Applied to spike data recorded during decision-making, our model revealed that populations of neurons encoded the same dynamic variable predicting choices, and heterogeneous firing rates resulted from the diverse tuning of single neurons to this decision variable. The inferred dynamics indicated an attractor mechanism for decision computation. Our results reveal a unifying geometric principle for neural encoding of sensory and dynamic cognitive variables.

Tuning curves of single neurons for sensory variables determine the geometry of the population code^{1,2}. This coding principle was established by mapping out changes in trial-averaged firing rates of neurons in response to varying parameters of sensory stimuli^{1,2,9}. For example, the orientation of a visual stimulus is a one-dimensional circular variable encoded in the primary visual cortex, where neural population responses organize on a ring mirroring the encoded variable^{2,10} (Fig. 1a). The orientation tuning curves of single neurons jointly define the embedding shape of this ring in the population state space, that is, the geometry of the population code¹ (Fig. 1a, Extended Data Fig. 1a and Supplementary Note 1.1).

However, whether the same geometric coding principle holds for dynamic cognitive variables is unknown. Internal cognitive processes (for example, decision-making or attention) are not directly observable and unfold with a unique time course on single trials in sparse and irregular spiking of neural populations^{3–8}. Thus, dynamic cognitive computations cannot be revealed by averaging neural responses over repeated trials. Moreover, individual neurons in association brain areas show diverse temporal response profiles during cognitive tasks^{11–15}, and the widespread assumption is that this heterogeneity reflects complex dynamics involved in cognition^{16,17}, implying that neural encoding of dynamic cognitive variables follows a fundamentally different principle than for sensory variables (Extended Data Fig. 1b and Supplementary Note 1.1).

Contrary to this view, we hypothesized that the complexity arises from the same coding principle as in sensory areas: the neural population dynamics encode simple cognitive variables, whereas individual neurons have diverse tuning to the cognitive variable, similar to neural tuning curves for sensory stimuli (Fig. 1b, Extended Data Fig. 1c

and Supplementary Note 1.1). To test our hypothesis, we developed a computational approach to simultaneously infer neural population dynamics on single trials and non-linear tuning functions of individual neurons to the unobserved population state. Two crucial technical advances within this approach make testing our hypothesis possible. First, we performed non-parametric inference over a continuous space of models to discover equations governing population dynamics directly from data^{18,19}, unlike previous methods that tested a small discrete set of models^{4,20,21}, without guarantees that any of these a priori chosen models faithfully reflect neural dynamics²². Second, the inference of non-linear tuning functions allows us to reconcile the diversity of single-neuron responses with the population-level encoding of a low-dimensional cognitive variable. By contrast, previous methods assume a rigid monotonic relationship between firing rates of all neurons and latent states and thus capture population dynamics with more latent dimensions, which may not directly correspond to the encoded cognitive variable^{23–27}.

We applied our approach to neural population activity recorded from the primate dorsal premotor cortex (PMd) during perceptual decision-making¹¹, a cognitive computation described by a decision variable reflecting the dynamics of choice formation on single trials^{28,29}. The neural representation of the decision variable remains unknown as its unique trajectories on single trials are not observable^{3,4}, and decision-related responses of cortical neurons are complex and heterogeneous^{8,11,20}. Our hypothesis states that neural population dynamics encode a one-dimensional decision variable, and heterogeneous neural responses arise from diverse tuning of single neurons to this decision variable (Fig. 1b). Using our computational approach, we provide three lines of evidence for our hypothesis: in dynamics of single

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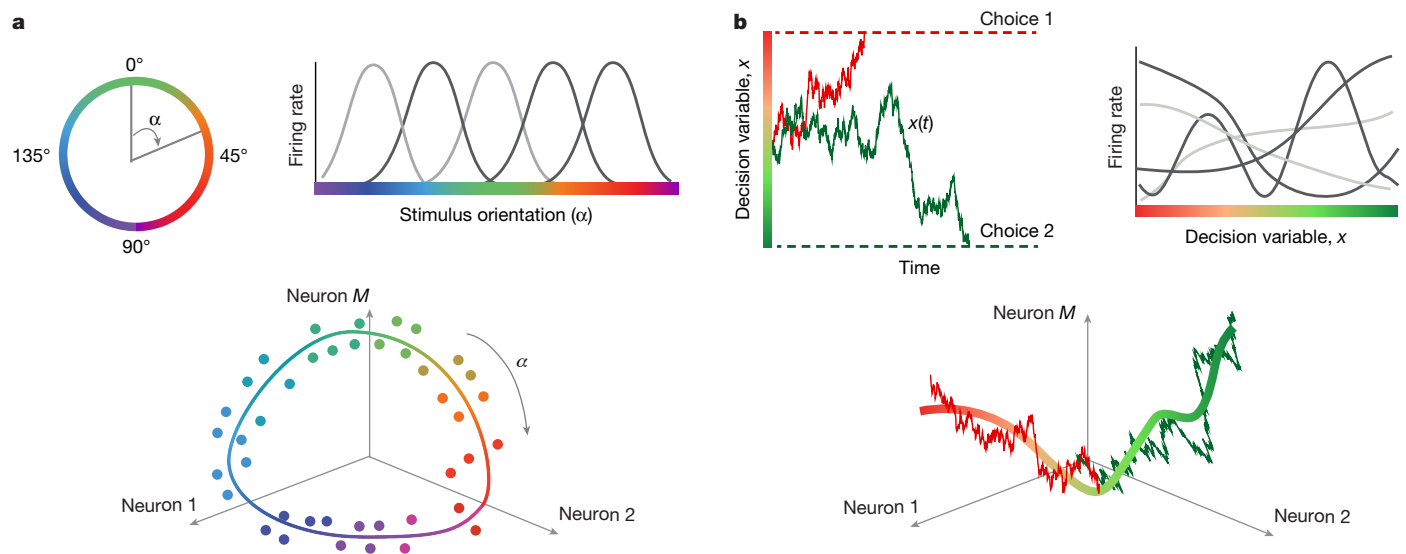


Fig. 1 | Neural population codes for sensory and cognitive variables.

a, Orientation of a visual stimulus is a one-dimensional circular variable α (top left). Single neurons in the primary visual cortex encode the orientation of a stimulus with bell-shaped tuning curves, which describe the trial-averaged firing rate of a neuron as a function of the stimulus orientation (top right). In the population state space, these neural responses form a ring mirroring the encoded variable (bottom; the dots denote trial-averaged population responses to different stimulus orientations indicated by colour, with the scatter illustrating estimation noise due to a finite number of trials; the line indicates the idealized noise-free ring manifold encoding the stimulus orientation). **b**, We hypothesize that the same geometric coding principle holds for dynamic cognitive variables. Specifically, a decision variable $x(t)$ is

a one-dimensional variable representing the dynamics of choice formation on single trials (top left; trajectories coloured by the final choice). Single neurons may encode the decision variable with diverse tuning functions, which describe the instantaneous firing rate of a neuron on single trials as a function of the decision variable value (top right). During decision formation, neural population responses evolve along a one-dimensional manifold encoding the decision variable, which is embedded in a high-dimensional neural population state space (bottom; noisy lines illustrate stochastic trajectories of the decision variable on two example trials coloured by choice, and the solid line indicates the idealized noise-free decision manifold). The tuning curves of all neurons jointly define the embedding shape of the decision manifold in the population state space, that is, the geometry of the neural population code for choice.

neurons, neural population dynamics and their correspondence with animal choices.

Neural recordings during decision-making

We analysed spiking activity recorded with linear multi-electrode arrays from the PMd of two monkeys performing a decision-making task¹¹ (Fig. 2a). The monkeys discriminated the dominant colour in a static checkerboard stimulus composed of red and green squares and reported their choice by touching the corresponding left or right target when ready (a reaction-time task). We varied the stimulus difficulty across trials by changing the proportion of the same-coloured squares in the checkerboard and grouped trials into four stimulus conditions according to the response side indicated by the stimulus (left versus right) and stimulus difficulty (easy versus hard; Fig. 2a; see Methods, ‘Behaviour and electrophysiology’).

Many single neurons in our recordings had decision-related responses with trial-averaged firing rates separating according to the chosen side (Fig. 2b). Although some neurons showed canonical firing rates ramping up or down with a slope dependent on the stimulus difficulty, most neurons exhibited heterogeneous temporal response profiles (Fig. 2b), seemingly incompatible with our hypothesis that all these neurons encode the same dynamic decision variable.

Flexible inference framework

To test our hypothesis, we developed a flexible modelling framework that dissociates the dynamics and geometry of neural representations and enables estimating both simultaneously in data (Fig. 2c; see Methods, ‘Flexible inference framework’). We modelled neural activity on single trials as arising from a dynamic latent variable $x(t)$. Each neuron i has a unique tuning function $f_i(x)$ to this latent variable, analogous

to tuning curves of single neurons to sensory stimuli (Fig. 1a). The tuning functions of all neurons jointly define the geometry of trajectories traced by neural activity through the population state space on single trials (Fig. 1b, Extended Data Fig. 1c and Supplementary Note 1.1). The dynamics of the latent variable $x(t)$ along these trajectories are governed by a general non-linear dynamical system equation^{18,19}:

$$\dot{x} = -D \frac{d\Phi(x)}{dx} + \sqrt{2D} \xi(t). \quad (1)$$

Here $\Phi(x)$ is a potential function that defines deterministic forces in the latent dynamical system, and $\xi(t)$ is a Gaussian white noise with magnitude D that accounts for stochasticity of latent trajectories. Our modelling framework can generate data with identical dynamics but different geometry, or vice versa (Extended Data Fig. 2), dissociating the dynamics of the latent variable $x(t)$ from the geometry of its representation within the population state space. By contrast, trial-averaged firing rates conflate the dynamics and geometry of neural representations; hence, the geometry of the trial-averaged population activity does not uniquely define dynamics on single trials^{4,30} (Extended Data Fig. 3).

To model decision-related activity, $x(t_0)$ was sampled from the distribution $p_0(x)$ of initial states at the beginning of each trial, and the trial terminated when $x(t)$ reached one of the decision boundaries in the latent space¹⁹ (Fig. 2c). We modelled spikes of each neuron i as an inhomogeneous Poisson process with the instantaneous firing rate $\lambda(t) = f_i(x(t))$ that depends on the current latent state $x(t)$ via the tuning function $f_i(x)$ (Fig. 2c). In our model, $\Phi(x)$, $p_0(x)$ and tuning functions $f_i(x)$ of all neurons are continuous functions that can take any non-linear shapes, enabling flexible discovery of both the low-dimensional latent dynamics and the non-linear geometry of single-trial trajectories in the population state space.

We simultaneously inferred the functions $\Phi(x)$, $p_0(x)$, $f_i(x)$ and the noise magnitude D from spike data by maximizing the model likelihood