Neural Dynamics in Dorsolateral Prefrontal Cortex Underlying Flexible Perceptual Decision-Making

Tian Wang, Kenji Lee, Nicole Carr, Chandramouli Chandrasekaran

Abstract

How neural dynamics in prefrontal cortex lead to flexible perceptual decisions is not fully understood. We trained monkeys to discriminate the dominant color (sensory input) of a red-green checkerboard and reached and touched a target that matched the dominant color of the checkerboard. Target configurations were randomized to decouple color choice signals from action choice signals. Neurons in DLPFC covaried more with target configuration and color choice compared to neurons in area 8 and dorsal premotor cortex (PMd). Neural trajectories in DLPFC first separated as a function of target configuration, and then after checkerboard onset separate by both color and action choice. To derive a mechanistic understanding, we trained a low-rank task recurrent neural network (RNN) model and found that its PC trajectories resembled those of DLPFC. Subsequent fixed-point analysis of the RNN suggest that the sustained inputs from the targets leads to two stable regions for target configuration and subsequent color inputs from the checkerboard leads to stable fixed points for the four possible combinations of color and action choice (e.g, red and left etc). Together, these results show that DLPFC likely mediates flexible perceptual decisions, and posit a candidate input-mediated dynamical mechanism.

Keywords: perceptual decision-making; prefrontal cortex; dimensionality reduction; recurrent neural network

Perceptual decision-making involves discriminating sensory input and selecting appropriate actions to achieve behavioral goals. However, depending on different contexts, the same sensory input might lead to different behavioral responses or different stimuli might prompt the same behavior (Okazawa & Kiani, 2023). Currently, we do not understand 1) which brain areas can support flexible decision-making, and 2) the neural mechanisms that lead to flexibility. We address these open questions by combining electrophysiological recordings in macaque monkeys, dynamical systems analysis and fixed-point structure of low-rank RNN task models.

DLPFC is a locus for flexible decision-making

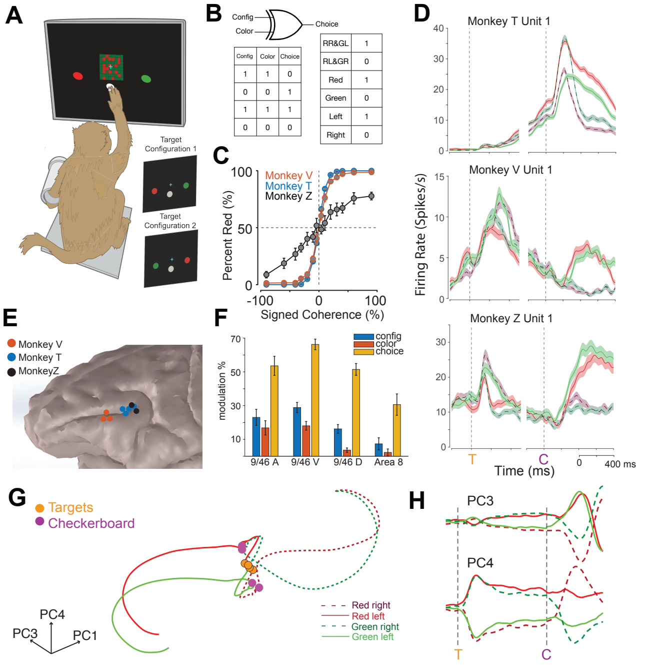

Figure 1: DLPFC neural dynamics likely mediates flexible perceptual decisions. **(A)** Behavioral task with two target configurations. Config1: red left & green right (RL&GL). Config2: red right and green left (RR&GL). **(B)** Choice is the XOR from color and target configuration. **(C)** Psychometric curve of each monkey as a function of checkerboard signed color coherence. **(D)** PSTH of example units. **(E)** Recording sites of Monkey V, T & V. **(F)** Percentage of units modulated to context, color and choice in each recording area (A: anterior; P: posterior; D: dorsal; V: ventral). Error bar: 99 percentile confidence interval **(G)** PCA trajectories of recorded units. **(G)** PC3 & 4 trajectories vs time.

We trained three macaque monkeys (T, Z, V) to perform a red-green checkerboard discrimination task that demands flexible association between sensory stimuli and actions (Fig. 1A, (Chandrasekaran, Peixoto, Newsome, & Shenoy, 2017)). In this task, monkeys discriminate the dominant color of a static checkerboard composed of red (R) and green (G) squares parameterized by 14 signed color coherences (R-G)/(R+G) ranging from almost all red (100%) to all green (-100%). Monkeys report their decision by touching the target of the corresponding color. We randomized the target configurations on a trial-by-trial basis and thus decoupled color choice (red vs. green) from action choice (left vs. right). Notably, the three task variables: target configuration (context), color, and action choice fulfills XOR constraints, where action choice can be computed by the XOR computation of context and color choice or vice versa (Fig. 1B). While the monkeys performed the decision-making tasks, we recorded single neuron spike signals within a wide range of DLPFC areas with linear multi-contact electrodes and neuropixels.

All three monkeys learned the task. Psychometric curves shown in Fig. 1C indicated monkeys made more errors for more ambiguous checkerboards. While animals performed this task, we recorded 3730 units (single neurons and multi-units) in DLPFC using V-probes and neuropixels from 170 sessions (118 in T, 19 in Z, and 33 in V).

Fig. 1D shows firing rates of example units in DLPFC averaged according to color choice and action choice. DLPFC neurons responded to the different target configurations (contexts), due to their selectivity to a combination of color and choice (red left and green right) after target onset. After the checkerboard onset, many units switched from encoding target configuration to encode all four possible combinations of color and action choice; and finally, the neural activities separated based on action choice. Selectivity for these various decision-related variables were found in all monkeys.

We recorded in a wide range of sites along the principal sulcus including rostral and caudal DLPFC, and area 8 (Fig. 1E), with recording areas verified based on MRI. We calculated the percentage of units modulated by each task variable within each recording area and found that color and context signal decreases along anterior-posterior and ventral-dorsal axes (Fig. 1F, errorbars denote 99% confidence intervals, chi-square test, $p < .001$ for color choice, target configuration and action choice). Color and target configuration effects were stronger in Anterior and DLPFCv compared to DLPFCd and area 8 (CIs do not overlap). The observed functional gradients were not an effect of performance differences among monkeys or sample size of different cortical areas as we only chose correct trials in the analysis. Depth-dependent differences were observed in single neuropixel sessions.

Neural population dynamics in DLPFC solve the XOR problem

We next examined the neural population dynamics in DLPFC underlying the XOR computation. Low dimensional neural trajectories derived from PCA on data pooled from all monkeys showed that trajectories separated based on target configuration and this signal sustained to checkerboard epoch (Fig. 1G-H). After the checkerboard onset, sensory evidence from color is combined with the target configuration input in DLPFC and leads to 4 fully separated neural trajectories according to both color choice and action choice and thus solving the XOR problem. Individual PCs were often mixtures of context and choice (PC3) or context and color (PC4). (Fig. 1H).

Low-rank RNNs suggest an input mediated dynamical mechanism

To understand the dynamical mechanisms underlying these flexible decisions in DLPFC, we trained low-rank RNNs models with varying ranks to preform the same task (Fig. 2A (Valente, Pillow, & Ostojic, 2022)). We found that the neural trajectories of the rank-4 RNN were the most similar to the real DLPFC data. The PCA on RNN firing rates generated similar results with neural trajectories separating based on target configuration after target onset and into 4 trajectories after checkerboard onset (Fig. 2B). The autonomous dynamics of the RNN only had a fixed point at the origin suggesting that the system is input driven. We next analyzed the regions of stability for the RNN while the inputs were present. After targets onset (black dots), each target configuration pushes the dynamics to a region of stability, setting up two distinct initial conditions (Fig. 2C). After the checkerboard onset (magenta dots), the color input further pushes the trajectories to two directions on each target configuration (Fig. 2D). As a result, 4 trajectories separates at the end of the trial according to all four combinations of color and action choice (e.g. red and left).

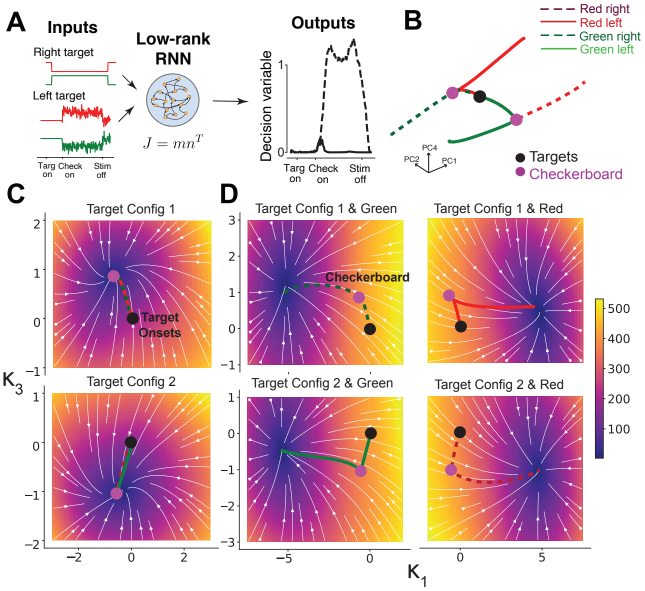

Figure 2: low-rank RNN simulation (rank=4) of the XOR task. **(A)** low-rank RNN schematic **(B)** PCA trajectories of the RNN recurrent units during the task. **(C)** vector fields and trajectories of the RNN from task beginning to checkerboard onset. **(D)** vector fields and trajectories from checkerboard onset to the trial end.

The low-rank RNN recapitulated dynamics observed in DLPFC. However, one difference is that color and target configuration are relatively over represented within the RNN while action choice signal is the strongest signal in DLPFC. In the brain, DLPFC has feedforward and feedback interactions between other brain areas including premotor cortex , while the RNN merely uses a nonlinear activation function to calculate action choice. A multi-area RNN in which the output of the first area is propagated to downstream areas will help address this question further (Kleinman et al., 2023)

Conclusion

Our study reveals that neural dynamics in the macaque DLPFC unmixes all the possible combinations of color and action choice thereby solving the nonlinear XOR problem, and thus flexible decision-making. DLPFC has stronger decision-related signals than areas such as area 8 (putative FEF) and PMd (data not shown). These results are a first of its kind in-vivo demonstration of a functional organization of the prefrontal cortex for perceptual decisions. Such a conclusion rests on using a task design where decision-making and motor preparation signals are deliberately uncoupled. Future work will 1) attempt to derive neuronal circuit motifs from these dynamics (Langdon & Engel, 2022), and 2) use residuals to assess if neural dynamics in the data match the dynamical mechanism in the model (Galgali, Sahani, & Mante, 2023).

References

Chandrasekaran, C., Peixoto, D., Newsome, W. T., & Shenoy, K. V. (2017). Laminar differences in decision-related neural activity in dorsal premotor cortex. *Nature communications*, *8*(1), 614.

Galgali, A. R., Sahani, M., & Mante, V. (2023). Residual dynamics resolves recurrent contributions to neural computation. *Nature Neuroscience*, *26*(2), 326–338.

Kleinman, M., Wang, T., Xiao, D., Feghhi, E., Lee, K., Carr, N., ... Kao, J. C. (2023). A cortical information bottleneck during decision-making. *eLife*. doi: 10.1101/2023.07.12.548742

Langdon, C., & Engel, T. A. (2022). Latent circuit inference from heterogeneous neural responses during cognitive tasks. *BioRxiv*, 2022–01.

Okazawa, G., & Kiani, R. (2023). Neural mechanisms that make perceptual decisions flexible. *Annual review of physiology*, *85*, 191–215.

Valente, A., Pillow, J. W., & Ostojic, S. (2022). Extracting computational mechanisms from neural data using low-rank rnns. *Advances in Neural Information Processing Systems*, *35*, 24072–24086.