Neural trajectories coding for time in precuneal neurons in the macaque

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Introduction

Understanding how the brain encodes the temporal order of episodic memories remains a central question in neuroscience. We investigated how the temporal order of episodic memory in the order of seconds is represented in macaque precuneal neurons, focusing on population-level neural dynamics during memory retrieval in a temporal order judgment (TOJ) task. By applying neural manifold learning techniques to the population activity, we uncovered a low-dimensional geometric structure that effectively represents temporal information from the memory task. This approach allowed us to visualize how the neural state evolves, revealing the underlying representation of remembered temporal order in the precuneus.

Method

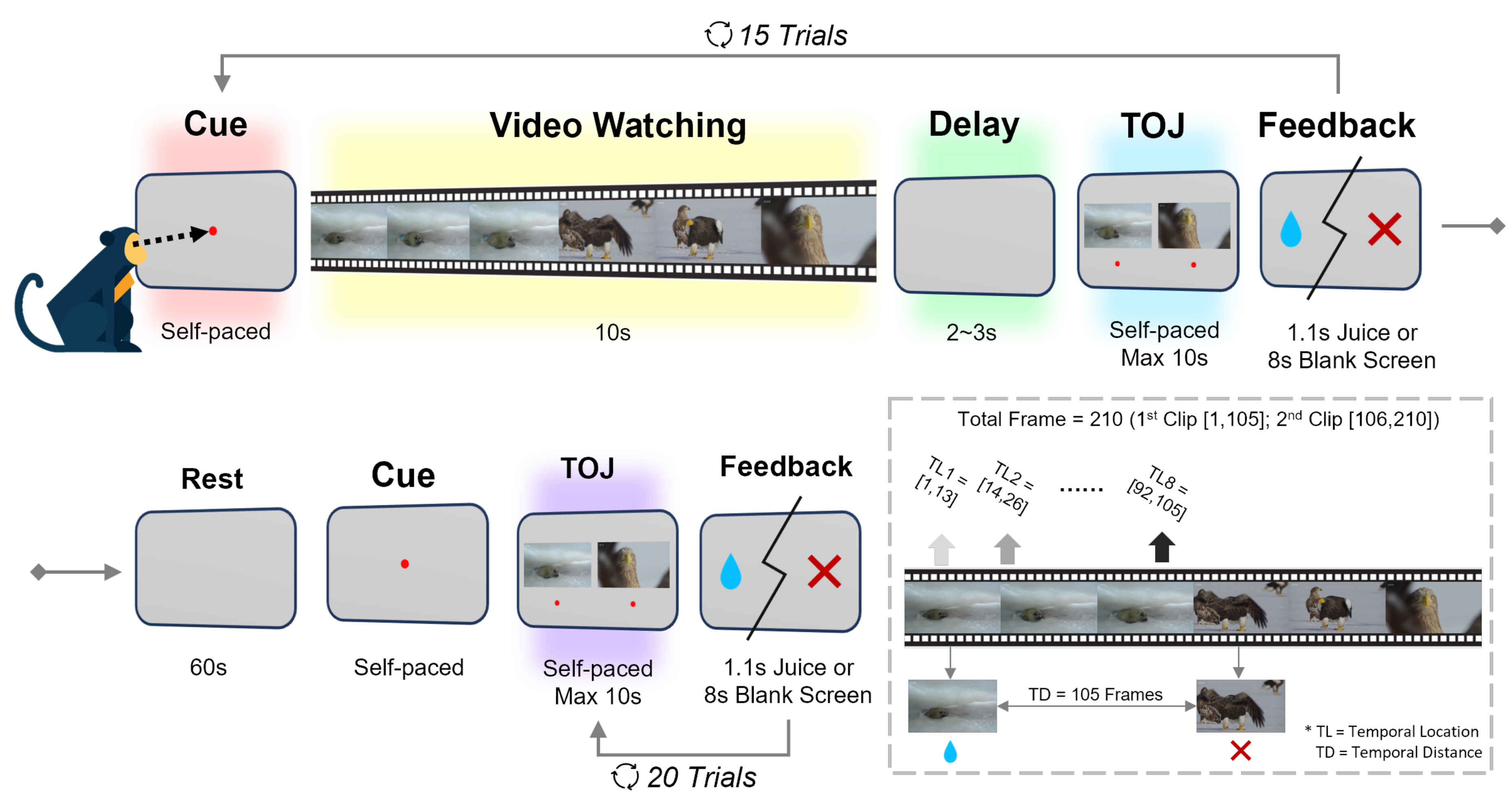

Fig. 1 Task paradigm of the temporal order judgement(TOJ) in macaque monkeys. The behavioral paradigm consisted of distinct learning and testing phases. Each trial began with the monkey holding gaze on a central fixation point. During the learning phase, subjects were presented with a 10s video stimulus, composed of two concatenated 5s clips. This was followed by a 2s delay period, after which two static images from the video were presented. The monkey had to make a two-alternative forced-choice (2AFC) judgment, indicating which image had appeared earlier in the sequence by shifting its gaze. The learning phase consisted of 15 trials, followed by a 1-minute rest interval. Subsequently, in the testing phase, the monkey performed 20 trials relying on the memory of the learned sequence. This entire session was conducted for four unique video stimuli each day.

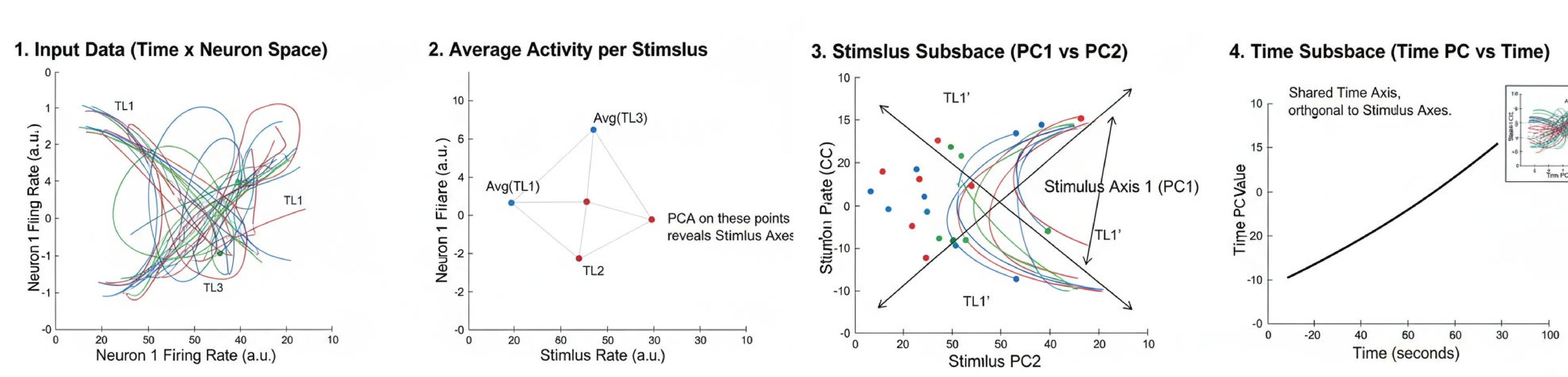

Fig. 2 Schematic of the Demixed PCA method. Demixed Principal Component Analysis (dPCA) is a dimensionality reduction technique that disentangles neural population activity into components related to experimental conditions and those reflecting shared temporal dynamics. The analysis begins with high-dimensional neural trajectories where condition-specific and time-varying signals are intermixed. By performing PCA on the time-averaged activity for each condition, the method identifies "Stimulus Axes" that maximally separate the conditions. Projecting the original data onto these axes separates the neural trajectories by condition, visualizing the stimulus-specific encoding. A "Time Axis" is then computed orthogonal to the stimulus subspace to reveal the shared temporal dynamics common across all conditions. Ultimately, dPCA provides an interpretable decomposition that allows for the independent analysis of what information the neural population encodes (the condition) and when it does so (the time).

Results

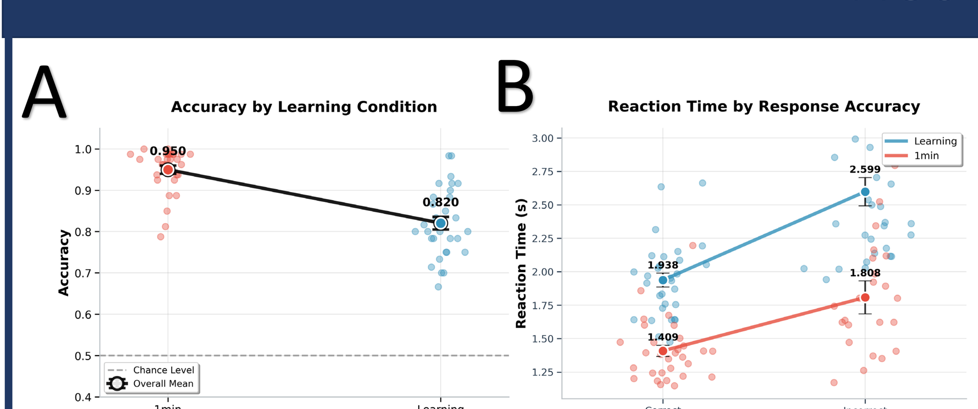

Fig. 3 Behavioral results for TOJ task. A. Mean accuracy. "Learning" and "1 min" denote the Learning phase and the testing phase after a 1-min rest. Monkeys performed well above chance level (0.5) in both phases. B. Mean reaction time. Blue indicates the Learning phase and red the 1-min test. Reaction times were consistently longer during Learning than during testing, regardless of accuracy. Light dots represent daily means across 30 sessions; error bars indicate SEM.

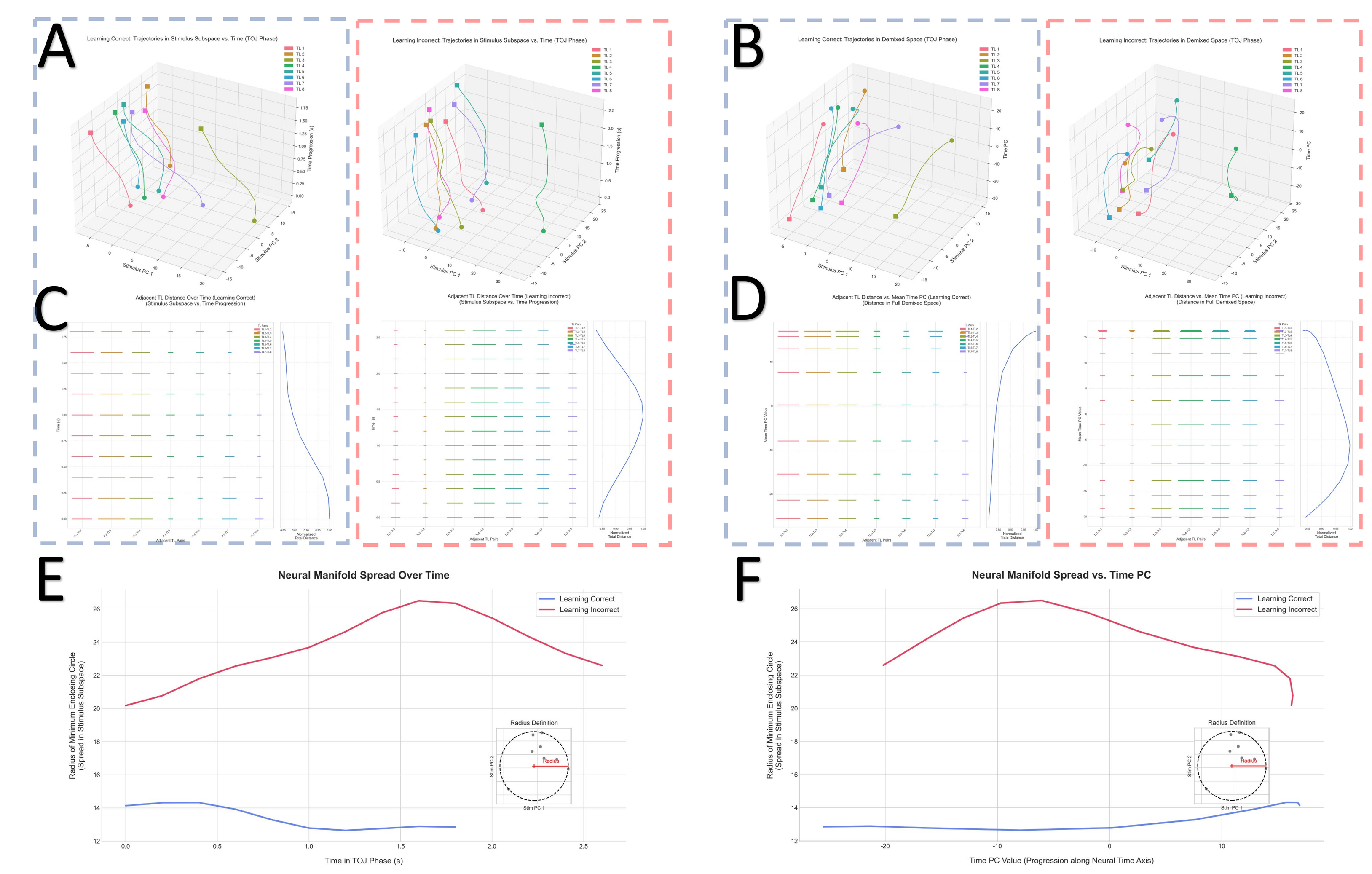

Fig. 4 Neural population dynamics during the initial learning phase. Neural dynamics during the initial learning phase for correct (blue) and incorrect (red) trials. Left column: analyses based on physical time (Time Progression). Right column: analyses based on intrinsic neural time (Time PC).(A, B) TOJ period trajectories appear similar in physical time (A), but in the intrinsic Time PC space (B), incorrect trials show increased curvature.(C, D) The distance between adjacent temporal locations (TLs) is less stable during incorrect trials in both Time Progression (C) and Time PC (D) coordinates.(E, F) The neural manifold radius expands more during incorrect trials in both views, indicating a less compact representation.

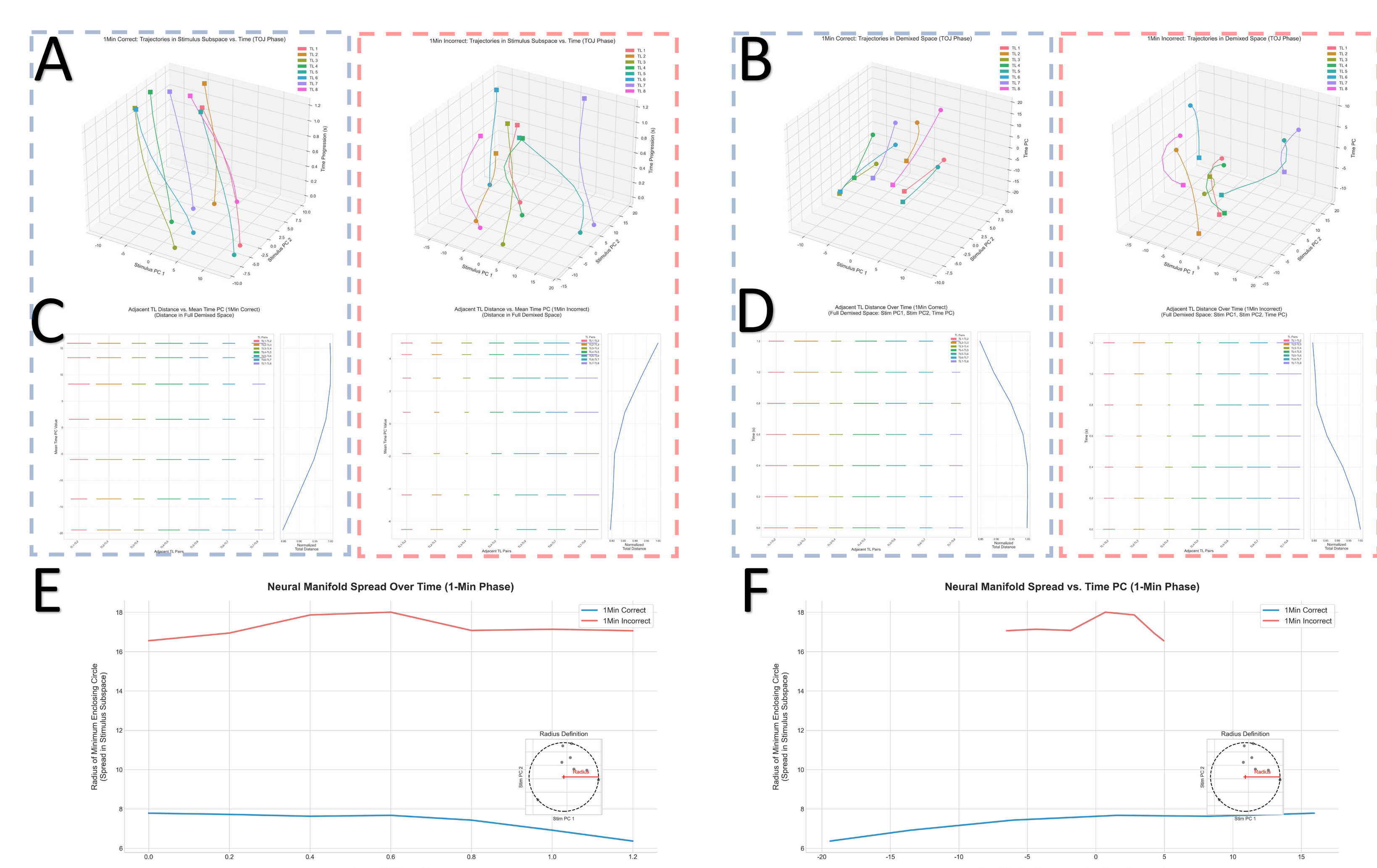

Fig. 5 Emergence of a Dichotomous Neural Manifold After Consolidation. Neural dynamics after a 1-minute consolidation period. A stark divergence emerges between correct (blue) and incorrect (red) trials, especially in the intrinsic Time PC space (right column).(A, B) While trajectories in physical time remain similar (A), the Time PC space (B) reveals a highly linear path for correct trials versus a convoluted path for incorrect trials.(C, D) TL separation for correct trials is stable for a prolonged period in physical time (C) and steadily increases in PC space (D). In contrast, this separation collapses for incorrect trials in both views.(E, F) The manifold radius for correct trials is stable over a long duration (F, large x-range), while for incorrect trials it is unstable and truncated (F, small x-range).

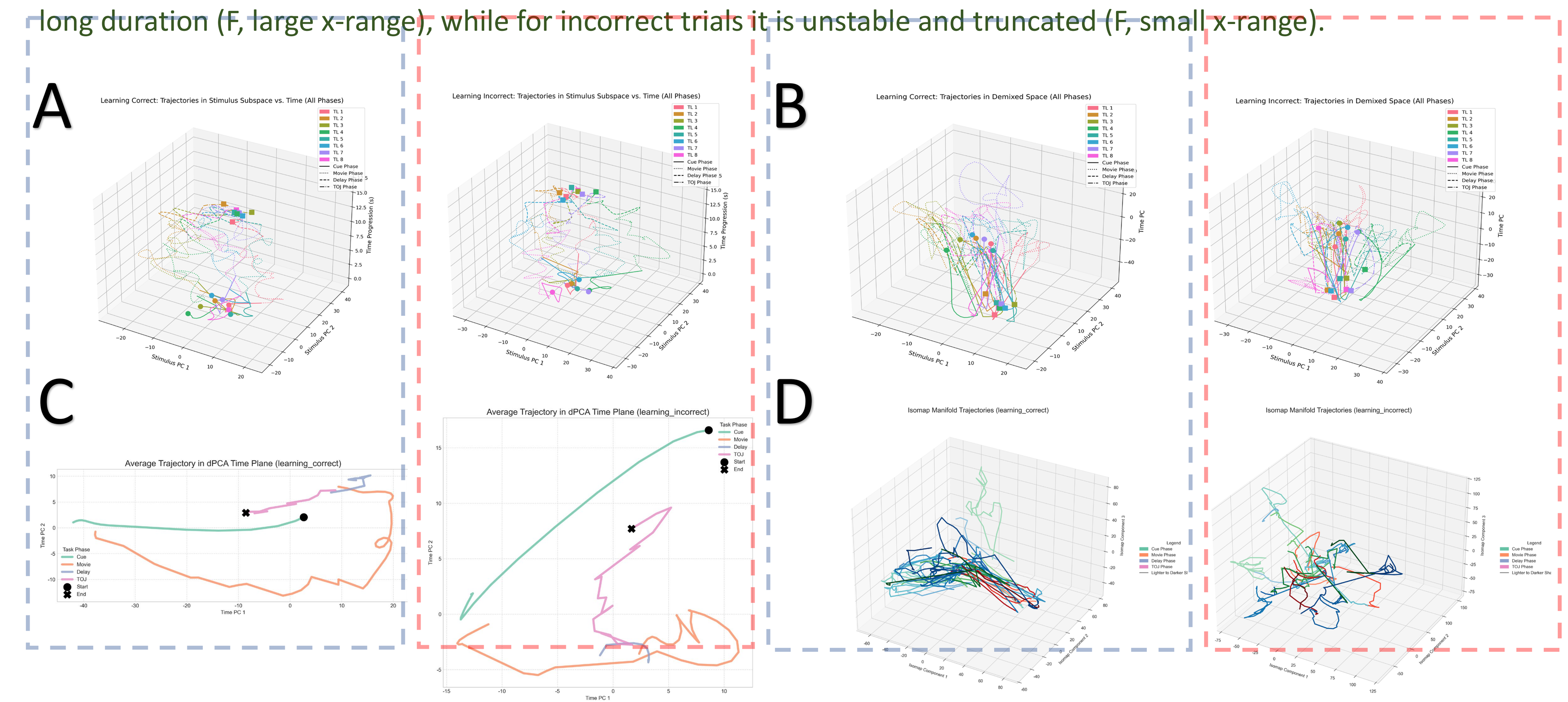

Fig. 7 Non-linear and State-Dependent Geometry of the Neural Manifold. Geometric structure of the neural manifold across the four task stages. In each panel (A-D), the left plot corresponds to correct trials and the right plot to incorrect trials.(A) Trajectories projected against physical time (Time Progression) show clear separation of the four task stages for both correct and incorrect trials.(B) When projected against intrinsic neural time (Time PC), stage separation is lost for both conditions, indicating the neural representation of time is non-linear.(C) The projection onto the stimulus plane (Time PC1 vs. Time PC2) reveals a highly structured, circular path for correct trials that is severely disorganized during incorrect trials.(D) Non-linear embedding with ISOMAP successfully segregates the four stages for correct trials but fails for incorrect trials where the manifold is tangled, confirming a collapse of the underlying geometric structure.

Conclusion

- The neural representation of time is an intrinsic, non-linear manifold, not a direct mapping of physical time.
- Task performance is directly linked to the geometric organization of the neural manifold, with errors corresponding to its collapse.
- Learning and consolidation refine the manifold's geometry, starkly separating the neural representations of correct and incorrect memories.

References & Funders

- Sarkar et al. arXiv 2024; Cao et al. PNAS. 2024

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