Initial conditions combine with sensory evidence to induce decision-related dynamics in PMd

Summary: We employed a dynamical systems perspective to bridge decision-related neural activity and decision-making behavior, a fundamentally unresolved problem. The dynamical systems approach posits that neural dynamics (X) are parameterized by a state equation ($dX/dt = F(X) + U$) with varying initial conditions (x_0) and that evolves in time by combining at each time step, recurrent activity (F) and inputs (U).

We considered different dynamical systems that make predictions about whether 1) initial conditions substantially predict subsequent dynamics and reaction time (RT) and/or choice, and 2) whether inputs are combined with initial conditions to lead to differences in choice-related dynamics. We evaluated which of the various dynamical mechanisms best described neural population activity by investigating neural population dynamics in the dorsal premotor cortex (PMd) of monkeys performing a red-green RT checkerboard discrimination task.

Prestimulus neural state, a proxy for the initial condition, predicted poststimulus neural trajectories and showed organized covariation with RT. Furthermore, faster RTs were associated with faster pre- and poststimulus dynamics as compared to slower RTs, with these effects observed within a stimulus difficulty. Poststimulus dynamics depended on both the sensory evidence and initial condition, with easier stimuli and "fast" initial conditions leading to the fastest choice-related dynamics whereas harder stimuli and "slow" initial conditions led to the slowest dynamics. Finally, changes in initial condition were related to the outcome of the previous trial, with slower pre- and poststimulus population dynamics and RTs on trials following an error as compared to trials following a correct response.

Models with initial conditions that are random or biased towards one choice, or with sensory encoding delays are inconsistent with these findings. Instead, these results suggest that decision-related activity in PMd are most consistent with a dynamical system where inputs combine with outcome-sensitive initial conditions that covary with eventual RT to induce decision-related dynamics.

Additional Detail: Based on prior research, we hypothesized the following candidate dynamical systems for decision-making: initial conditions covary with RT ($x_0 \sim$ RT), RT and choice, or are random with a stimulus encoding delay as a function of stimulus difficulty (*Fig. 1A*). We tested which of these dynamical systems best described neural activity in PMd of two macaque monkeys discriminating the dominant color of a central, static checkerboard composed of red (R) and green (G) squares who reported their decisions with arm movements (*Fig. 1B*). There were seven levels of stimulus difficulty parameterized by color coherence (|R-G|/(R+G)) (*Fig. 1B*). Discrimination accuracy increased and mean RT decreased with increasing coherence for both monkeys (*Fig. 1C*). However, coherence explained only ~12.4% and ~1.4% of RT variability in monkeys 1 and 2 respectively. RTs for trials after errors were also slower than RTs for trials after correct responses.

While monkeys performed this task we recorded 996 single and multi-units from PMd (monkey 1: 546 units from 75 sessions; monkey 2: 450 units from 66 sessions). PMd neurons were heterogeneous and demonstrated complex time varying patterns of activity during the task (*Fig. 1D*).

Subsequent analyses using dimensionality reduction, trajectory analysis, and decoding revealed that the initial condition (measured as the prestimulus neural state) predicted the evolution of poststimulus neural trajectories (speed and location[1]) and RT but not eventual choice (*Fig. 1E,F,G*). Faster RTs were associated with faster pre- and poststimulus dynamics as compared to slower RTs (*Fig. 1F*). Ultimately, both sensory evidence (*Fig. 2A*) and initial condition (*Fig. 2B*) modulated poststimulus dynamics, with choice selectivity greatest for "fast" initial conditions and easy stimuli, and latency dependent on RT bin for the hardest stimuli (*Fig. 2C,D,E*).

Finally, we investigated if fluctuations in the prestimulus state were linked to the previous trial's outcome. Neural activity in principal component (PC) space separated by the previous trial's outcome before stimulus onset (*Fig. 2F*) and a KiNeT[1] demonstrated slower pre- and poststimulus dynamics (*Fig. 2G*) and RTs in trials following an error as compared to trials following a correct response. Future analyses will investigate the structure of single-trial dynamics and test the hypothesis that post-error trials are 'slower' due to an initial condition further from a movement onset state and/or developing along a more circuitous path (*Fig. 2H*).

Our findings naturally bridge previously disparate findings from speed-accuracy tradeoff, post-error adjustment, motor planning and timing research, providing a common framework for deriving models of neural computations underlying decision-making.

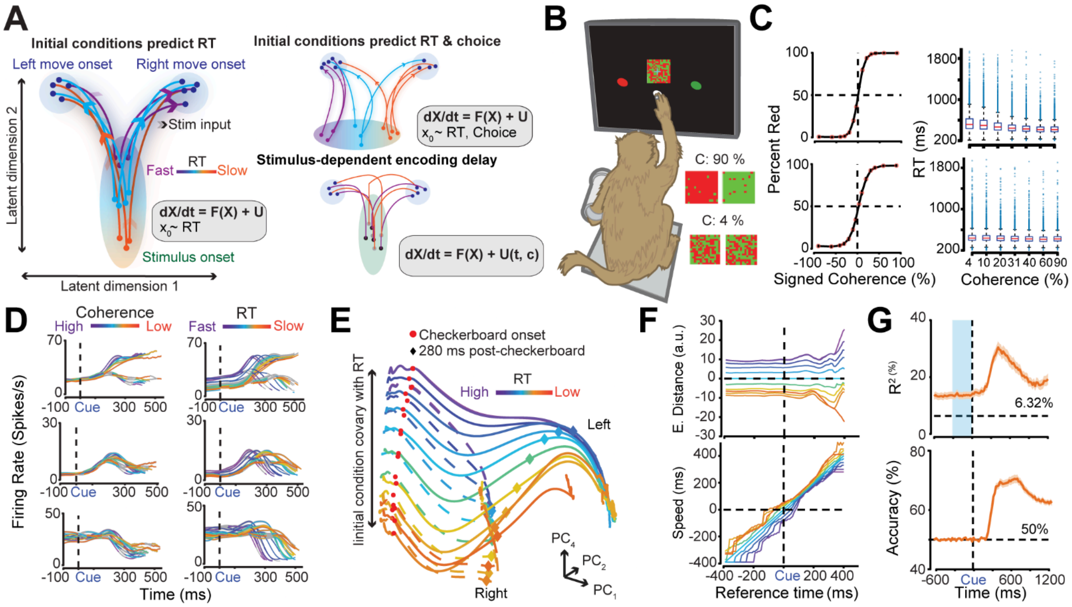

Figure 1: **Prestimulus neural activity covaries with RT but not choice:** **(A)** Dynamical systems where position and velocity of the initial condition and the sensory evidence have varying effects on RT and choice. **(B)** Behavioral task and example stimuli. **(C)** Psychometric curves and RT distributions. **(D)** Average firing rate of three heterogenous neurons (rows) organized by coherence (left) and RT (right) and aligned to checkerboard onset (Cue). **(E)** State space trajectories (PCs 1,2,4) of average firing rate of units organized by choice and RT demonstrating prestimulus neural covariation with RT. **(F)** KiNeT[1] Euclidean (E.) distance and speed analyses show that pre- and poststimulus trajectories are organized by RT bin and are faster for faster RTs as compared to a reference trajectory (light blue, middle trajectory). **(G)** Regression and decoding analysis show prestimulus spiking activity is predictive of RT (R^2) but not choice.

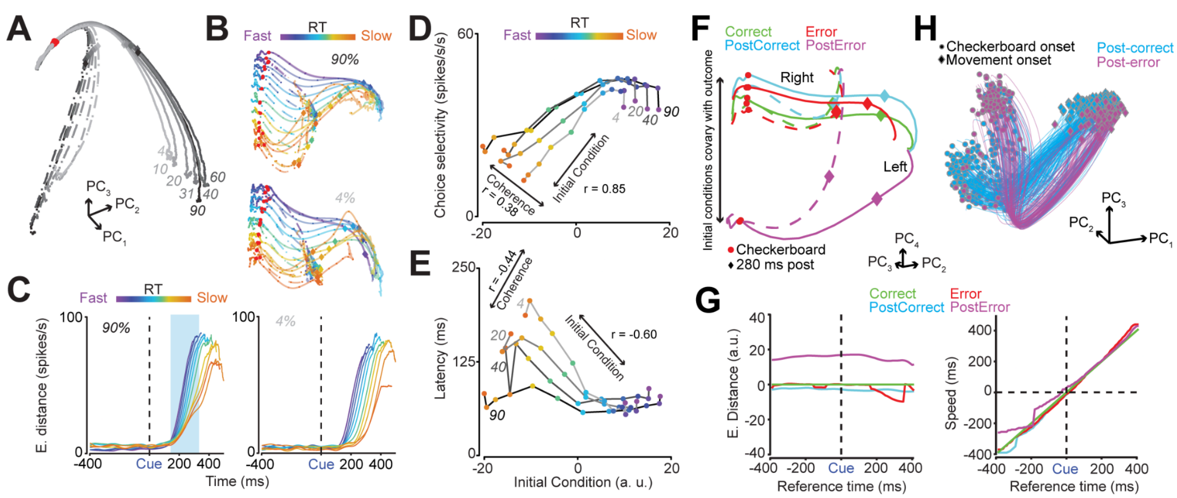

Figure 2: **Initial conditions and sensory evidence determine choice neural dynamics:** **(A)** Poststimulus dynamics are shaped by sensory evidence. **(B)** State space trajectories organized by choice and RT within a stimulus coherence maintain prestimulus neural covariation with RT and choice dynamics. **(C)** Choice selectivity (average Euclidean distance between left and right reaches, blue highlight box) separates faster for faster RT bins as compared to slower RT bins. **(D)** Rate at which the choice selectivity signal grows (see **C**) depends on *both* coherence and initial condition (first component of PCA of 200 ms period before checkerboard onset of neural activity organized by coherence, RT bins, and choice). **(E)** When choice selectivity emerges (i.e., latency) is flat across RT bins for the easiest coherence (90%) but is increasingly dependent upon initial condition as stimuli increase in difficulty. **(F)** Post-error trials demonstrate the largest separation in initial condition in a state space for averaged firing rates organized by choice and trial outcome. **(G)** KiNeT[1] Euclidean (E.) distance and speed analyses showing that initial conditions separate as a function of the previous trials outcome and that neural trajectories are slower after an error trial (violet) as compared to correct trials (light green). **(H)** LFADS[2] trajectory of post-correct and post-error trials demonstrating prestimulus separation in state space and post-error trials having more curved trajectories.

[1] Remington et al., 2018, Neuron, [2] Pandarinath et al, 2018, Nature Methods