

Initial conditions in dorsal premotor cortex covary with RT, are altered by trial outcome, and combine with sensory evidence to induce decision-related reach dynamics

How the time-varying and heterogeneous responses of neural populations drive decision-making behavior is a fundamentally unresolved problem. Recent motor planning and timing studies have leveraged a “dynamical systems” perspective to succinctly describe and understand behaviorally-relevant neural computations. Here, we investigated if such a perspective could bridge decision-related neural dynamics and behavior.

The dynamical systems perspective posits that neural computations are described by a state equation that evolves in time by combining recurrent activity and inputs. Distinct neural state space trajectories (i.e., dynamics) can emerge due to variation in initial conditions, inputs or both. Our two key predictions from this approach are that 1) initial conditions, sensitive to the previous trial’s outcome, substantially predict the speed and location of subsequent dynamics and behavior¹ and 2) sensory evidence (i.e., inputs) combines with initial conditions to affect the speed of decision-related dynamics (*Fig. 1A*).

To test these predictions, we trained two monkeys to perform a red-green reaction time (RT) checkerboard discrimination task. Monkeys discriminated the dominant color of a central, static checkerboard composed of red (R) and green (G) squares and reported their decisions with arm movements (*Fig. 1B*). The sensory evidence was varied across seven levels of stimulus difficulty parameterized by color coherence ($|R-G|/(R+G)$). Discrimination accuracy improved and mean RT decreased with increasing coherence for both monkeys (*Fig. 1C*). However, coherence explained only ~10% and ~1% of RT variability in monkeys 1 and 2 respectively. Additionally, trials after errors had slower RTs than trials after correct responses. While monkeys performed this task we recorded 996 single neurons and multiunits from the dorsal premotor cortex (PMd, monkey 1: 546 units from 75 sessions; monkey 2: 450 units from 66 sessions).

PMd neurons 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 location²) and behavior, specifically RT but not eventual choice (*Fig. 1E,F,G,H*). Faster RTs were associated with faster pre- and poststimulus dynamics as compared to slower RTs (*Fig. 1F*). Ultimately, both initial condition and sensory evidence modulated poststimulus dynamics (*Fig. 2A*), 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 (*Fig. 2B,C,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 decoder, using current trial spiking activity, predicted the previous trial’s outcome above chance levels before stimulus onset. These results suggest that the initial condition was altered by the outcome of the previous trial, with slower pre- and poststimulus dynamics (*Fig. 2G*) and RTs in trials following an error as compared to trials following a correct response. Alterations in the prestimulus state caused by errors likely lead to a shift towards a slower RT state as revealed by a demixed principal component analysis (dPCA)⁴ analysis where axes that maximally separated for RT and outcome were significantly aligned (~50°). Future analyses will investigate the structure of single-trial dynamics and test the hypothesis that post-error trials are ‘slower’ due an initial condition further from a movement onset state and/or developing along a more circuitous path (observe curvature of post-error trajectories, *Fig. 2H*).

These results suggest that neural activity in PMd is well described by a dynamical system where inputs combine with outcome-sensitive initial conditions to induce decision-related dynamics. 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.

[1] Afshar et al., 2011, Neuron, [2] Remington et al., 2018, Neuron, [3] Pandarinath et al, 2018, Nature Methods, [4] Kobak et al, 2016, eLife

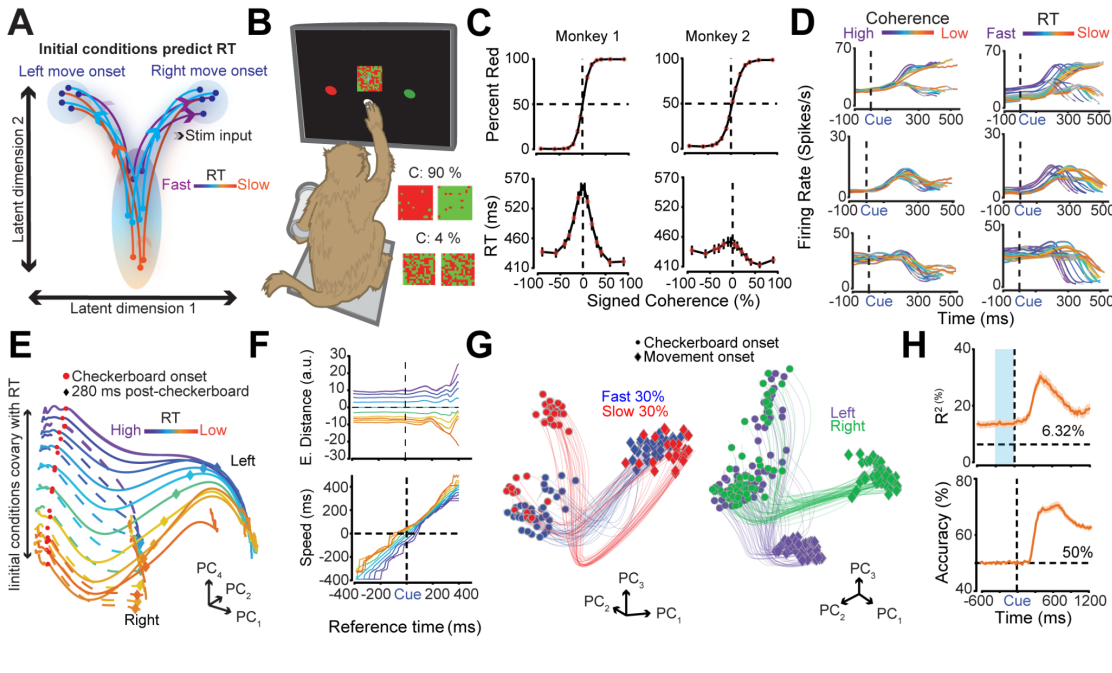


Figure 1: Prestimulus neural activity covaries with RT but not choice: (A) Hypothesis: the position and velocity of a neural state at the time of stimulus onset¹ and the coherence of the stimulus input negatively correlate with RT. (B) Behavioral task and example stimuli. (C) Psychometric curves and RT distributions as a function of signed coherence: $(R-G)/(R+G)$. (D) Average firing rate of three 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. Observe separation of trajectories by RT bin prior to checkerboard onset. (F) Kinematic analysis of neural trajectories (KiNet)² distance (Euclidean (E.) distance) and speed analyses showing that neural trajectories lawfully organize by RT bin and that pre- and post-stimulus neural trajectory speed is faster for faster RTs as compared to a reference trajectory (middle RT bin, cyan/middle trajectory). (G) Latent factor analysis via dynamical systems (LFADS)³ single-trial neural (23 units from one session) trajectories for 90% coherence demonstrate that the fastest and slowest 30% of trials are mostly separate prior to checkerboard onset (left) but that left and right reaches are intermixed at checkerboard onset (right). (H) Variance explained (R^2) by linear regressions on 20 ms bins of spiking activity and coherence (6.32% - variance explained by coherence alone) to predict RT and accuracy of logistic classifier built on 20 ms bins of spiking activity to predict choice (50% - chance performance). Spiking activity is predictive of RT prior to checkerboard (Cue) onset (blue highlight box) but not choice.

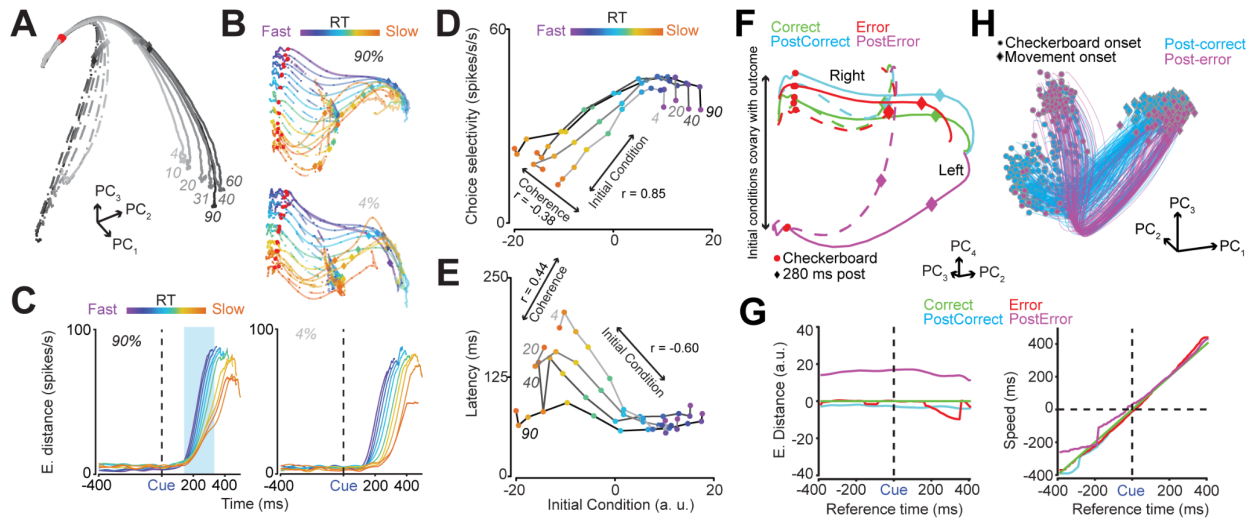


Figure 2: Initial conditions and sensory input determine choice neural dynamics: (A) State space trajectories (PCs 1-3) of average firing rate of units organized by choice and coherence. (B) Dynamics separate as a function of RT bin prior to checkerboard onset and demonstrate consistent poststimulus structure regardless of coherence (same as Fig 1E but organized within a coherence). (C) Euclidean (E.) distance between left and right reaches as a function of 11 RT bins. Choice selectivity separates faster for faster RT bins as compared to slower RT bins (blue highlight box). (D) Rate at which the choice selectivity signal grows (see C) is dependent upon *both* initial condition (first component of PCA of neural activity organized by coherence, RT bins, and choice of a 200 ms period before checkerboard onset) and coherence. (E) When choice selectivity emerges (latency) is mostly flat for all initial conditions for the easiest coherence (90%) but is increasingly dependent upon initial condition as the stimuli decrease in coherence. (F) State space trajectories for averaged firing rates organized by choice and previous trial's outcome. Post-error trials demonstrate the largest separation in initial condition as compared to all other trial types. (G) KiNet² distance (Euclidean (E.) distance) and speed analyses showing that neural trajectories separate as a function of the previous trials outcome and that pre- and post-stimulus neural trajectories are slower after an error trial (violet) as compared to the reference trajectory (light green, correct trials). (H) LFADS³ trajectory of post-correct and post-error trials.