The Neural Dynamics of Dynamic Decisions

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Most research on decision-making focuses on static situations in which an agent is faced with a choice that is constant over time, such as discriminating sensory stimuli with stable informational content. However, the brain evolved to make decisions in real-time during ongoing activity in a highly dynamic world, in which the options themselves as well as their risks and payoffs are continuously changing. To investigate the neural mechanisms of such dynamic decisions, we trained monkeys to perform a reach-decision task (Fig. 1a) in which they observe 15 tokens jumping one-by-one every 200ms from the center to one of two targets and must guess which target will ultimately receive the majority. Importantly, the decision can be made at any time and then the remaining tokens jump more rapidly, motivating a speed-accuracy tradeoff. From behavioral data, we hypothesized that monkeys quickly calculate the evidence provided by the tokens and combine it with a growing "urgency signal" and commitment is made when the product of the two reaches a critical level. Indeed (Fig. 1b), many cells in dorsal premotor (PMd) and primary motor cortex (M1) are tuned prior to the time of the decision and continuously reflect the temporal profile of evidence combined with elapsed time. About 280ms before movement onset, PMd cells tuned to the selected target hit a consistent peak of activity that we believe signals the moment of commitment(*1*).

Our previous analyses focused on a subset of cells that were significantly tuned prior to decision time. However, cortical populations are highly heterogeneous and do not neatly partition into clear categories such as "decision" or "movement cells". Thus, inspired by recently developed methods(*2*), here we sought to analyze the activity of the entire population by plotting the dynamical state of the system as a trajectory through a high-dimensional neural space. Because our recordings were not performed simultaneously, we could not plot individual trials but classified them according to the temporal profile of sensory information, defining what we called "easy", "ambiguous", and "misleading" trials (Fig. 1b, top), computed for movements to the left or right targets. Each cell's activity was aligned on movement onset, binned (20ms), square-root transformed, averaged across trials of each class, and then smoothed with a 25ms Gaussian. Neural trajectories for each trial class were computed in a high-dimensional space defined by orthogonal axes corresponding to each cell's activity and then remapped into a low-dimensional space using Principal Components Analysis. Thus, instead of averaging across cells we averaged across similar trials and plotted activity in a space that reflected the major features of the evolving neural trajectory.

The first 6 principal components (PCs) explained 85% of the variance in the data and further improvements were quite gradual. As shown in Fig. 2, these components appear to be functionally interpretable: PC1 signals the transition between deciding and moving, PC2 reflects the evidence for the left or right target, and PC3 resembles our hypothesized "urgency signal". Fig. 3a shows the neural trajectories plotted in the space of the first 3 PCs (70% of total variance). During deliberation, the neural state evolves upon a 2-dimensional "decision manifold" defined by orthogonal directions roughly corresponding to sensory evidence and urgency, and then rapidly falls off this surface at the moment of commitment into trajectories specific to each choice. This is consistent with a dynamical attractor network that implements decisions through a winner-take-all process. Interestingly, the decision manifold of the PMd population (Fig. 3b) is curved and leans away from commitment (upper inset), suggesting that PMd activity is pulled away from the attractor by inhibitory processes. In contrast, the decision manifold in M1 (Fig. 3c) is remarkably planar and leans toward commitment (upper inset), suggesting that M1 activity is continuously pushing the system to make a choice. Furthermore, while the decision surface in PMd is more strongly extended along the evidence (PC2) than the urgency dimension (PC3), the opposite is true for M1 (Fig. 3b,c, lower insets). We speculate that these phenomena reveal major features of the dynamics of neural populations during dynamic decision-making, while higher PCs (e.g. 5 and 6) reveal an orthogonal turn that signals the moment of commitment.

Finally, we found that the "loading matrix", which quantifies how each cell contributes to these PCs is a continuous distribution, without distinct clusters. This does not support the idea of separate functional groups but instead suggests that the entire PMd/M1 population may work together to govern the dynamics of decision-making. Nevertheless, certain trends exist, such as the different shapes and orientations of decision manifolds in PMd versus M1, suggesting at least a partial division of labor: M1 continuously pushes the system to decide and act while PMd pulls it away from committing until the neural state falls into an attractor.

1. D. Thura, P. Cisek, *Neuron* **81**, 1401 (2014).
2. B. M. Yu *et al.*, *J Neurophysiol* **102**, 614 (2009).

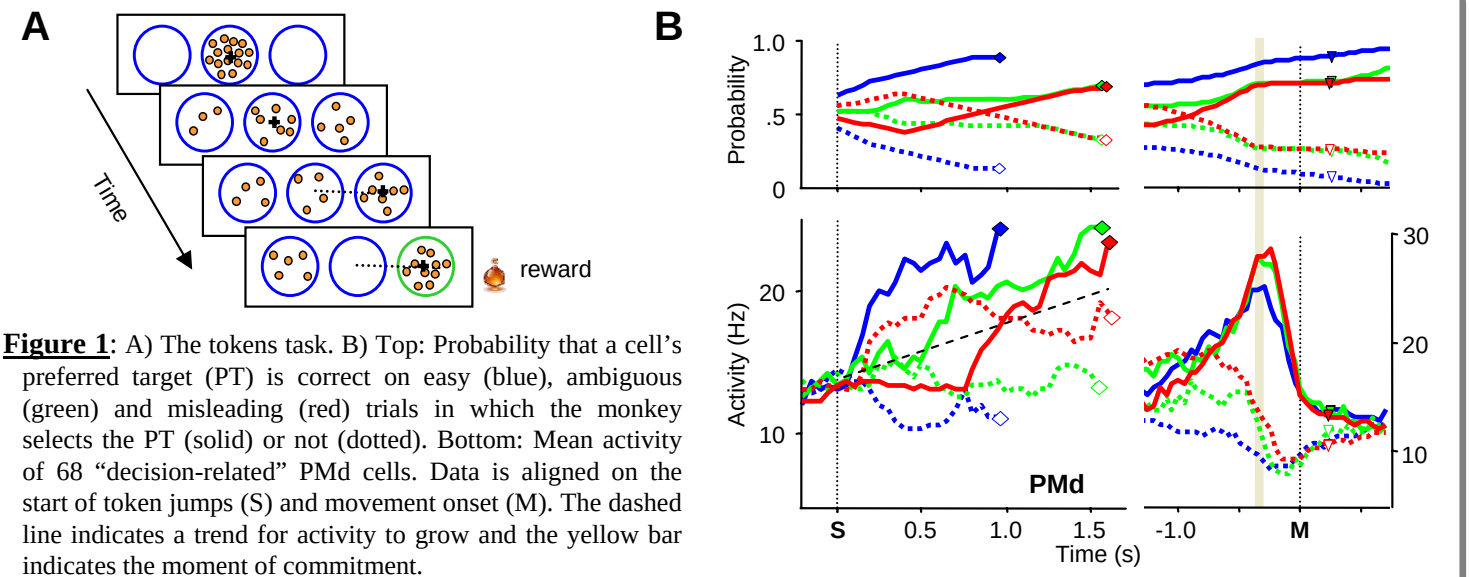

Figure 1: A) The tokens task. B) Top: Probability that a cell's preferred target (PT) is correct on easy (blue), ambiguous (green) and misleading (red) trials in which the monkey selects the PT (solid) or not (dotted). Bottom: Mean activity of 68 "decision-related" PMd cells. Data is aligned on the start of token jumps (S) and movement onset (M). The dashed line indicates a trend for activity to grow and the yellow bar indicates the moment of commitment.

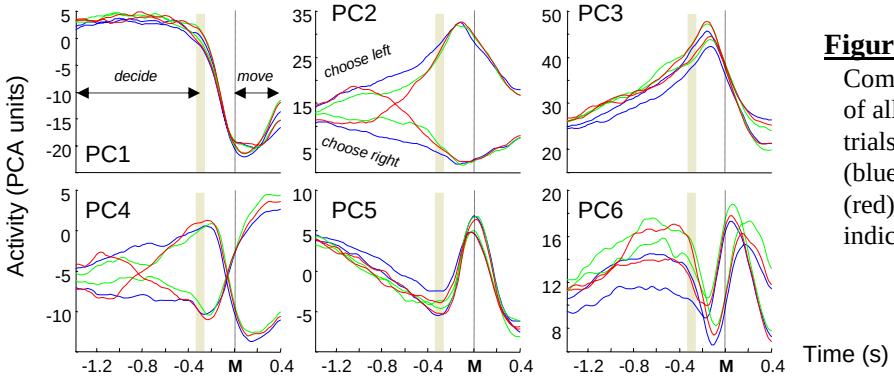

Figure 2: Temporal profiles of the first 6 Principal Components (PCs) derived from the firing activity of all PMd and M1 cells with a sufficient number of trials (N=384). Separate profiles are shown for easy (blue), ambiguous (green) and misleading trials (red) toward the right or left targets. Yellow bars indicate the estimated moment of commitment.

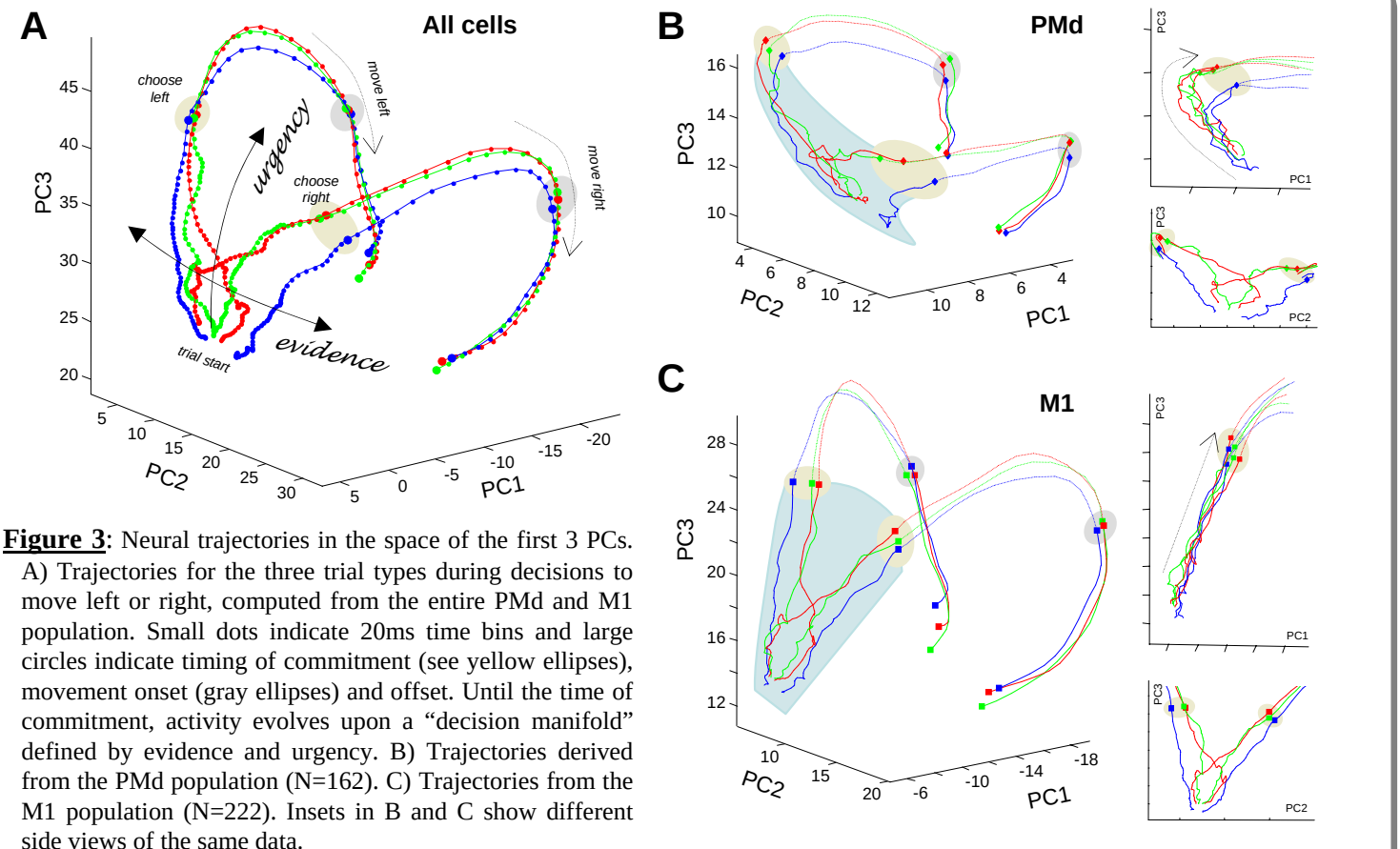

Figure 3: Neural trajectories in the space of the first 3 PCs. A) Trajectories for the three trial types during decisions to move left or right, computed from the entire PMd and M1 population. Small dots indicate 20ms time bins and large circles indicate timing of commitment (see yellow ellipses), movement onset (gray ellipses) and offset. Until the time of commitment, activity evolves upon a "decision manifold" defined by evidence and urgency. B) Trajectories derived from the PMd population (N=162). C) Trajectories from the M1 population (N=222). Insets in B and C show different side views of the same data.