Identifying the control priorities of monkeys and humans in a virtual balancing task

Summary: Primate neurophysiology has provided numerous insights into the neural mechanisms of short and stereotypical movements, such as center-out reaching, which are mainly guided by feedforward control. However, to understand highly interactive and feedback-driven behaviors, experimental paradigms are needed that involve continuous interactions with the world. One example of such paradigms is stick-balancing which requires constant integration of feedback for successful control. Recently, a simplified virtual implementation of the stick-balancing task was developed as the Critical Stability Task (CST), where monkeys and humans learned to balance an unstable system in a virtual environment. However, the control strategies to accomplish the task, as well as its neural underpinnings, remains to be examined. In theory, the task could be performed based on various control policies by prioritizing either the control of position or velocity of the system. This distinction, however, is particularly challenging to identify in the data as the unstable nature of the task leads to unique behavior at each attempt, with potentially different control policies at different trials. These variations render trial-averaging methods unsuitable as they fail to capture trial-specific control strategies. Here, we propose a generative-model approach at the level of behavior that successfully accounts for the behavioral features of monkeys and humans who performed the task under matching conditions. The model makes further predictions about the effect of different control strategies on how the task could be accomplished. These predictions were used to identify, at the single-trial level, the control priorities most likely used by monkeys and humans in each trial. These results provide a critical step towards understanding the neural activity associated with highly interactive sensorimotor behavior, and how such activity might represent different control priorities in the motor system.

Task and data: The Critical stability task (CST) involved balancing an unstable system, displayed as a cursor on the screen, using the hand movement. The dynamics of the system was governed by a first-order differential equation, $\dot{x} = \lambda(x + p)$, where x and p represented the cursor position and the hand position, respectively (Fig.1A). The movement trajectories of the hand and cursor are shown for two example trials in Fig.1B. The difficulty of the task was manipulated by changing the constant λ: larger λ meant higher level of difficulty. The trial was considered successful if the cursor remained within the bounds of the workspace ($\pm$5cm from the center) for six consecutive seconds. Behavioral data from two monkeys ([1]) and four human subjects was collected under matching conditions. Each human subject performed the task in three sessions of ~80 trials for different levels of task difficulty.

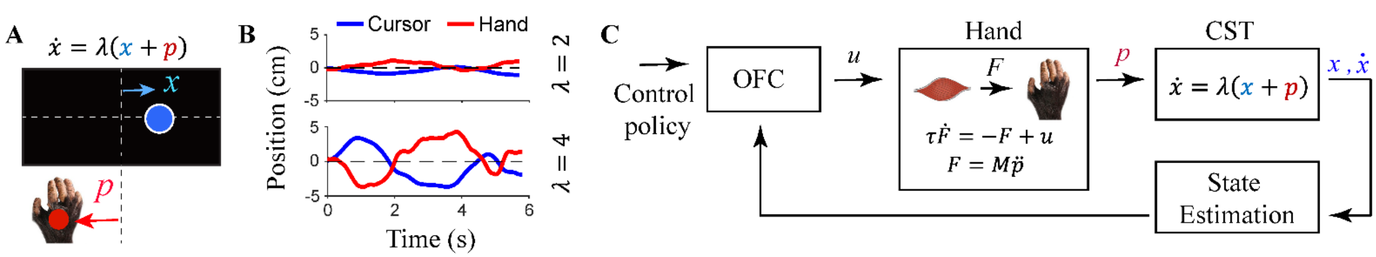

Fig. 1: **A**. The Critical Stability Task. **B**. The time course of cursor and hand position during two example trials of a monkey, for easy (top) and hard (bottom) levels of difficulty. **C**. A generative model based on optimal feedback control theory was developed to assess different control strategies underlying the behavior.

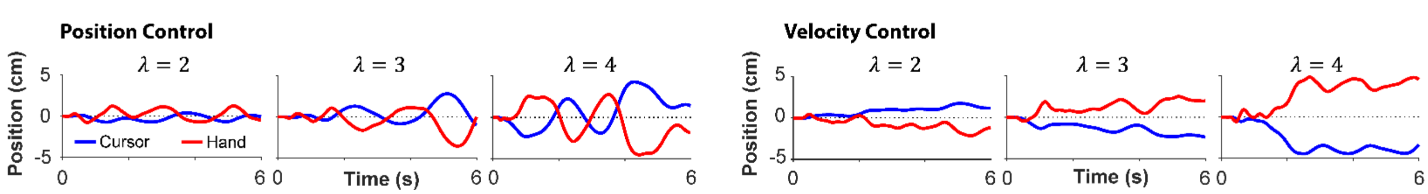

Fig. 2: Simulated trials based on position control (left) and velocity control (right) strategies.

Modelling and Results: We developed a model based on Optimal Feedback Control theory (OFC; [2]) that was adapted to perform the CST. The model received cursor position and cursor velocity as sensory feedback, and given the control policy, generated appropriate "hand" movement to accomplish the task. Two main control policies were examined: position control (bringing the cursor to the center of the screen), and velocity control (keeping the cursor still regardless of its position).

The model generated similar behavior to experimental data for both position- and velocity-based control strategies as exemplified in Fig. 2. Furthermore, the main features of behavior were successfully captured at the average level of performance for both humans and monkeys. As shown in Fig. 3, the model accounted for success rate, hand-cursor correlation, and the sensorimotor lag between hand and cursor movement as a function of task difficulty (λ). Importantly, the qualitative distinction between position and velocity-based control policy depicted by the model (Fig. 2) could also be identified in the experimental data. Fig. 4A illustrates example trials of two human subjects, where one exhibits patterns similar to position control policy (S1), while the other's behavior resembles that of a velocity control strategy. In Fig. 4B, the model makes distinct predictions about the joint distribution of cursor position and cursor velocity during the task for each control policy. By taking the average position and average velocity of the cursor for each trial, the model predicts a large correlation between these quantities under a velocity-based control (cyan), but not under a position-based control (yellow). The behavior shown for subjects S1 and S2 are each consistent, respectively, with position and velocity-based control as suggested by the model. Similar distinction is observed for the distribution of the cursor RMS during each trial (Fig. 4B, bottom panels).

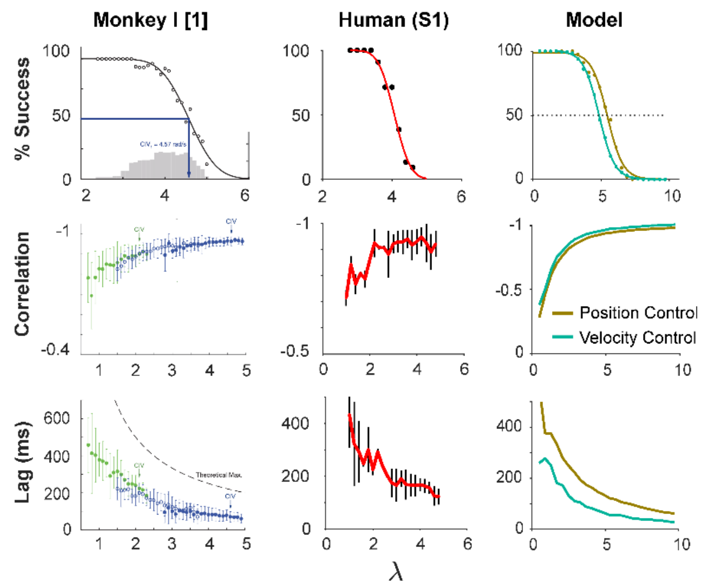

Fig. 3: The model accounts for the success rate, hand-cursor correlation, and hand-cursor lag observed in monkey and human data as a function of task difficulty (λ).

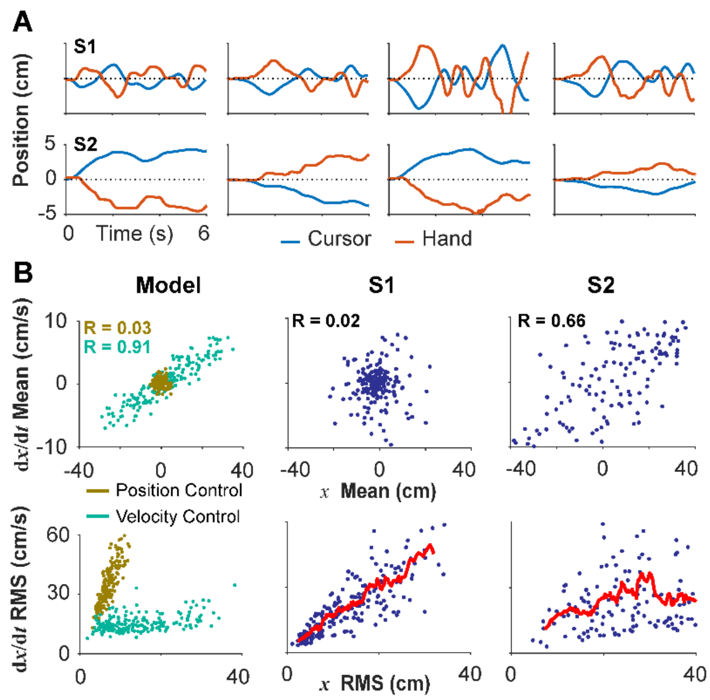

Fig. 4: **A**. Sample trials of two human subjects. **B**. Joint distribution of cursor position and cursor velocity for the mean (top) and RMS of the cursor time series. Each data-point is one trial. The model predicts separate distributions for position vs. velocity-based control strategies.

Conclusion: Our results present a powerful tool to identify different control policies used by humans and monkeys to accomplish a virtual balancing task. This is a critical step towards analyzing the neural activity associated with highly interactive sensorimotor behavior and investigating how such activity might represent different control priorities.

References:

[1] Quick KM, Mischel JL, Loughlin PJ, Batista AP, (2018) The critical stability task: quantifying sensory-motor control during ongoing movement in nonhuman primates. J Neurophysiol., Vol. 120, No. 5.

[2] Todorov E, (2005) Stochastic optimal control and estimation methods adapted to the noise characteristics of the sensorimotor system. Neural Comput. 17:1084–1108.