Inferring control objectives in a virtual balancing task in humans and monkeys

Mohsen Sadeghi[1,2*], Reza Sharif Razavian[3*], Salah Bazzi[1,2,4], Raeed Chowdhury[5], Aaron Batista[5], Patrick Loughlin[5], Dagmar Sternad[1,2,4,6]

[1] Departments of Biology, [2] Electrical and Computer Engineering, [6] Physics, and the [4] Institute for Experiential Robotics, Northeastern University, Boston, MA, USA.
[5] Department of Bioengineering, and Center for the Neural Basis of Cognition, University of Pittsburgh, PA, USA.
* Equal contribution

Impact statement

A computational approach identifies control strategies in humans and monkeys to serve as basis for analysis of neural correlates of skillful manipulation.

Abstract

Natural behaviors have redundancy, which implies that humans and animals can achieve their goals with different control strategies. Given only observations of behavior, is it possible to infer the control strategy that the subject is employing? This challenge is particularly acute in animal behavior because we cannot ask or instruct the subject to use a particular control strategy. This study presents a three-pronged approach to infer an animal's control strategy from behavior. First, both humans and monkeys performed a virtual balancing task for which different control strategies could be utilized. Under matched experimental conditions, corresponding behaviors were observed in humans and monkeys. Second, a generative model was developed that identified two main control strategies to achieve the task goal. Model simulations were used to identify aspects of behavior that could distinguish which control strategy was being used. Third, these behavioral signatures allowed us to infer the control strategy used by human subjects who had been instructed to use one control strategy or the other. Based on this validation, we could then infer strategies from animal subjects. Being able to positively identify a subject's control strategy from behavior can provide a powerful tool to neurophysiologists as they seek the neural mechanisms of sensorimotor coordination.

Introduction

Almost all actions in daily life can be achieved in multiple ways that all can lead to the desired task goals. As an example, consider a driver steering a car on a curvy road. She may choose different paths depending on whether she wants to maintain a consistent distance from the median strip or whether she aims to minimize changes in velocity. Both strategies can take the driver to her destination, maybe even arriving at the same time, although the precise path taken by the car in both situations will differ. How could one identify the underlying control objectives from differences in observed behavior? A considerable number of studies in human movement neuroscience have aimed to identify the control strategies in a given task based on their kinematic manifestations (Braun et al., 2009; Izawa et al., 2008; Nagengast et al., 2009; Razavian et al., 2023; Uno et al., 1989; Wong et al., 2021). However, experimental tasks are often chosen to elicit consistent behavioral features across repetitions and individuals, not only to facilitate analysis, but also to constrain control to a single objective. Behavior in natural settings, however, is often complex and highly variable across repetitions, and individuals can employ a multitude of strategies to accomplish a task. To date, understanding of such variable behavior - let alone its neural bases - has posed formidable challenges (Croxson et al., 2009; Diedrichsen et al., 2010; Kawato, 1999; Scott, 2004).

Attempts to understand the neural underpinnings of control objectives have been pursued in research on both humans and non-human primates (Benyamini & Zacksenhouse, 2015; Cross et al., 2023; Croxson et al., 2009; Desrochers et al., 2016; Kao et al., 2021; Miall et al., 2007; Nashed et al., 2014; Omrani et al., 2016). Yet, these two lines of inquiry have remained largely parallel with few direct bridges: human behavioral and computational research has mainly focused on the analysis of behavior, while animal research has used invasive methods such as intracortical recordings to gain direct insights into the neural mechanisms of movement control. Experiments with humans tend to use detailed experimental manipulations to elicit features of motor behavior that afford insights into its governing principles. Using a wide range of tasks, from simple reaching to interacting with complex objects, mathematical models with specific control algorithms have been used to reproduce the salient features of behavior (Crevecoeur et al., 2019; Diedrichsen, 2007; Nagengast et al., 2009; Nayeem et al., 2021; Razavian et al., 2023; Yeo et al., 2016). However, understanding the neural underpinnings of movement control at the intracortical level in healthy humans has remained a challenge. On the other hand, animal research, in particular with non-human primates, allows sophisticated methods to directly record neural activity to afford insights into neural correlates of motor behavior. Ultimately, this knowledge should transfer to how the human brain functions (Badre et al., 2015), but those links must be built.

To achieve this objective, cooperative study designs between human and animal motor research are needed to understand the neural basis of human motor skill (Badre et al., 2015; Rajalingham et al., 2022). However, there are difficult challenges to overcome: First, cooperative design requires matching behavioral tasks that can be performed similarly and with the same conditions by both humans and animals. The most appropriate animal model for many human behaviors are monkeys. Second, the goals and constraints of behavioral studies with monkeys and humans are somewhat different, which can preclude a direct comparison. Behavioral tasks used with monkeys are typically simpler than those used with humans, due to the animals' more limited cognitive capacities. Also, studies with monkeys aim for highly repeatable behaviors to facilitate the examination of neural activity by aggregating it across trials or days. In contrast, studies of human behavior can push toward tasks that are more cognitively sophisticated and that capture the complexity that abounds in natural activities. This study bridges the

78   gap between human and monkey behavioral studies to build toward an understanding of the neural
79   principles of human motor control.

80   We used an experimental paradigm, the Critical Stability Task (CST), that can be performed by both
81   humans and monkeys (Quick et al., 2018). The CST requires the subject to balance an unstable virtual
82   system governed by a very simple dynamical equation (see Met hods). Performing the task is akin to
83   balancing a virtual pole. The CST has features that make it suitable for the study of more complex motor
84   behaviors. First, while the goal remains the same, the difficulty of the task can be titrated. Second, it
85   involves interactions with an object (albeit virtual in our case) so that continuous adjustments are
86   required to succeed. Each trial evokes unique behavior that may reflect different control strategies to
87   accomplish the task. In addition, even if the same control strategy is employed, each trial generates
88   different behavior due to sensorimotor noise and the task's instability. As in the car driving analogy, the
89   subjects might seek to optimize position, or they might seek to optimize velocity, and different
90   behavioral strategies may lead to equal success.

91   Because of its complexity and redundancy, each trial of the CST is unique. The goal of the study is to
92   infer the subject's control policy (i.e., optimize position or optimize velocity) from observations of their
93   behavior. When the subjects are humans, it is possible to instruct them to employ a particular strategy
94   or to ask them posthoc what strategy they adopted to succeed at the task. This explicit route is
95   definitely not available with monkeys. As we are still quite far from 'reading out' strategies from neural
96   activity, we need to start with behavior to infer the control strategies. Hence, this study adopted a
97   computational approach based on optimal control theory to simulate behavior during the CST in various
98   conditions. This approach allowed us to make predictions about the behavioral signatures associated
99   with different control policies, which we then used to analyze the experimental data from both humans
100   and monkeys.

101   In overview, this study investigated, through experimental data and model-based simulations, the
102   sensorimotor origins of behavioral strategies in humans and non-human primates performing the CST.
103   We developed the experimental paradigm such that humans and monkeys executed the task under
104   matching conditions while recording movement kinematics in exactly the same way. An optimal control
105   model was used to simulate different control objectives, through which we identified two different
106   control strategies in the experimental data of humans and monkeys. We discuss how in the future these
107   results could guide the analysis of neural data collected from monkeys to understand the neural
108   underpinnings of different control policies in an interactive feedback-driven task with redundancy.

Results

110   The Critical Stability Task (CST) involved balancing an unstable system using horizontal movements of
111   the hand to keep a cursor from moving off the screen (**Figure 1**A, C). This study collected data from
112   human subjects performing the CST and compared it to previously collected data from monkeys
113   performing the same task. The hand's displacements were recorded by 3D motion capture (Qualisys,
114   Gothenburg), with a reflective marker attached to the hand. The cursor dynamics were generated by a
115   linear first-order dynamical system, relating hand and cursor kinematics as described in Quick et al.,
116   2018:

$$\dot{x} = \lambda(x + p) \qquad\qquad (1)$$

117 where x and $\dot{x}$ are the horizontal cursor position and cursor velocity on the screen, p is the horizontal
118 hand position, and λ is a positive constant fixed at the beginning of each trial. The parameter λ sets the
119 gain of the system. When λ is larger, the cursor would tend to move faster, making the task more
120 difficult as faster and more precise hand movements were required to maintain balance.
121 Correspondingly, success rates at the task decreased with increasing λ. To summarize the skill of human
122 and monkey participants, we identified the value at which subjects succeeded at only 50% of the trials
123 and defined that value as the "critical" λ.

124 The task goal was to keep the cursor within a range of space shown on the screen, i.e., $-c \leq x(t) \leq c$,
125 where c was a positive constant. This created a redundancy in achieving the task goal as there were
126 infinitely many ways in which one could balance the cursor inside the specified region. We examined
127 movement kinematics to identify control strategies employed by different subjects, or across different
128 trials.

129 In a previous study, two Rhesus monkeys were trained to perform the CST under increasing difficulty
130 levels (Quick et al., 2018). Similarly, here 18 human subjects were recruited to perform the same task
131 under comparable experimental conditions as the monkeys (see Methods). **Figure 1** illustrates the
132 experimental setup for both monkeys and humans (**Figure 1**A and 1C) and shows examples of their
133 behavior (**Figure 1**B and 1D). Overall, there were similarities in performance between humans and
134 monkeys. To further quantify and compare this performance across humans and monkeys, we defined a
135 set of control metrics to assess different aspects of control as detailed in the following.
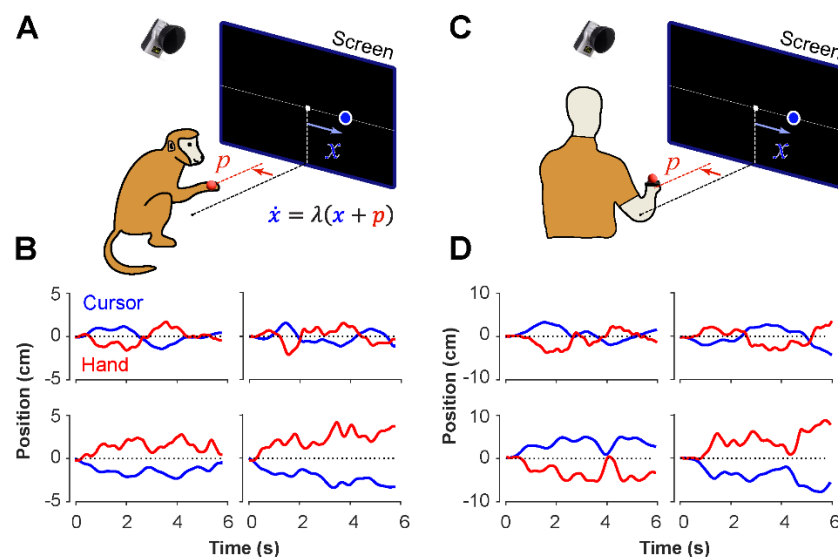
136

137 *Figure 1: Experimental setup for monkeys and humans performing the CST. Monkeys (**A**) and humans (**C**) controlled an*
138 *unstable cursor displayed on a screen using lateral movements of their right hand. The hand movements were recorded using*
139 *motion capture; the data were used in real-time to solve for the cursor position and velocity through the CST dynamics equation.*
140 *Timeseries of the hand (red) and cursor (blue) movements shown for four example trials from monkeys (**B**) and humans (**D**).*

Experiment 1: CST performance without instructed strategy

142 In the first experiment, six human subjects performed the CST with the only instruction to "perform the
143 task without failing to the best of your ability". Failure occurred if the cursor escaped the boundaries of
144 the screen (±10cm from the center) within the trial duration of 6s. Subjects received categorical
145 feedback about the outcome at the end of each trial in a text appearing on the screen reading "Well

146   done!" for success, and "Failed!" for failure. The degree of difficulty, set by λ, was increased stepwise
147   across trials until the subject could no longer perform the task (see Methods for the specifics about the
148   setting of λ values).

149   We first sought to examine the main characteristics of behavior in CST performance and how it
150   compared between humans and monkeys. To quantify the overall behavior, four main metrics were
151   employed as described and motivated below. To begin, we considered the overall success rate in the
152   task among different individuals, before focusing on the kinematics of task performance. **Figure 2**A
153   illustrates the success rates and how they dropped as the task difficulty increased. Both humans and
154   monkeys showed a similar pattern of decrease in success rate which was well-captured with a sigmoidal
155   function. Expectedly, individuals varied in their ability to achieve high difficulty levels as a measure of
156   skillful performance, indicated by their "critical λ value", that is, the value of λ when the success rate
157   drops below 50%. To investigate the performance in more detail, the kinematics of movement were
158   examined, specifically the hand and cursor position during each trial. As indicated in equation (1), the
159   hand position p was the control input to the system which aimed to control the cursor position x as the
160   variable of interest. Due to the unstable nature of the task, drifting of the cursor towards the edge of the
161   screen demanded a response by a hand movement to avoid failure. As such, two simple metrics
162   characterized control, one quantifying how the movement of hand and cursor correlated, and a second
163   one to what degree the hand response lagged cursor displacements. **Figure 2**B shows the correlation
164   between the cursor movement and the hand movement as a function of task difficulty. The strength of
165   the correlation increased as trials became more challenging in both monkeys and humans, asymptoting
166   towards −1. According to equation (1), this behavior was equivalent to reducing the sum $(p + x)$ when
167   λ increased, so as to prevent rapid changes in cursor velocity $\dot{x}$, and, hence, reduce the chance of failure.

168   The response lag from the cursor movement (observed feedback) to the hand movement (control
169   response) is an important characteristic of a control system. As shown in **Figure 2**C, by increasing the
170   task difficulty λ, the lag decreased for all subjects, meaning subjects generated faster corrective
171   responses to cursor displacements in more difficult trials. A possible reason for such behavior is that
172   higher λ values meant increased instability of the system, which required faster responses to avoid
173   failure. Whereas in easy trials, due to slower dynamics of the system, subjects could afford delayed
174   responses to cursor displacements (and hence, larger lags) and still manage to succeed.

175   As the fourth metric, we also calculated the control gain by measuring the ratio of root mean squared
176   (RMS) of hand position to the RMS of cursor position for each trial. This measure determined to what
177   extent the control signal (hand movement) compared in magnitude to the cursor movement. A large
178   gain meant that on average across a trial, the hand exhibited larger movements than necessary to
179   correct for cursor deviations. **Figure 2**D illustrates the calculated gain as a function of task difficulty for
180   humans and monkeys. As shown, except for *Monkey J*, the gain showed a gradual decrease as the task
181   difficulty increased for most individuals. Such decrease could be due to larger cursor movements at
182   higher difficulty levels, and perhaps more efficient corrective hand responses to cursor displacements.
183   To the latter, it is worth noting that for high λ values, small hand movements could cause large cursor
184   displacements, which was detrimental to the task success. Therefore, pruning any task-irrelevant hand
185   movements, consistent with promoting efficiency, seemed essential to succeed in more difficult trials.
186   Overall, the control metrics presented in **Figure 2** give insight into how the CST was performed: as the
187   task difficulty increased, subjects tended to respond to cursor displacements faster (that is, with lower
188   lag), more precisely (seen in the stronger hand-cursor correlation), and more efficiently (with lower

189 gain). Behavior was comparable between humans and monkeys, which suggests that there were
190 underlying control strategies used in common by both species. Next, we sought to detect those control
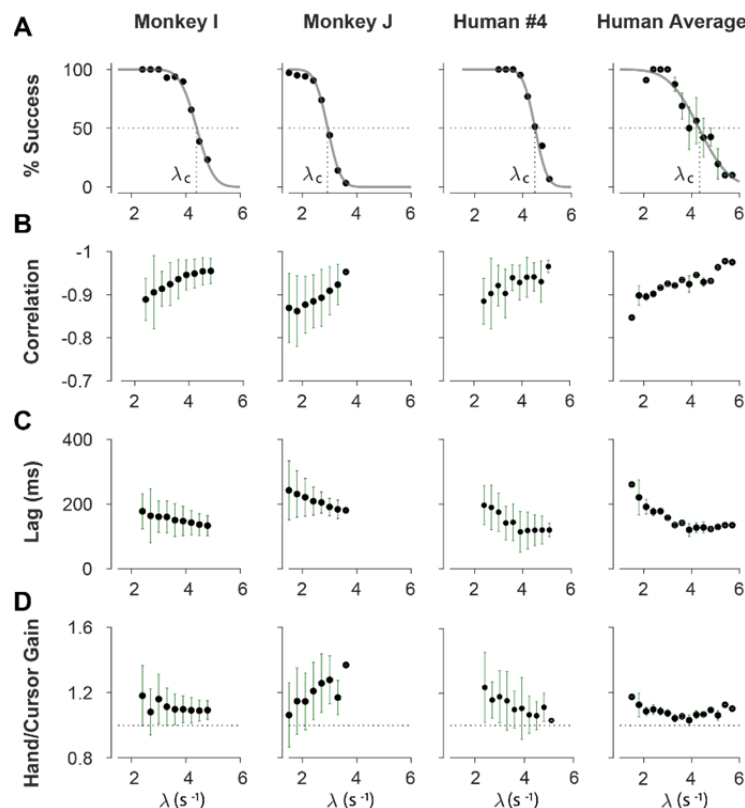191 strategies.

192

193 *Figure 2: Overall behavioral characteristics of CST performance as a function of task difficulty (λ). Data is shown for two*
194 *individual monkeys (first two columns from left) from a previous study* (Quick et al., 2018), *as well as an example human*
195 *individual (third column from left) and the average across human subjects (right-most column). For the individual subjects, each*
196 *data point and its corresponding error bars represent the mean±SD across trials for any given difficulty level, respectively. For*
197 *the human average plot, the data points and their corresponding error bars represent the mean±SE across individuals for each*
198 *difficulty level.* **A.** *Psychometric curves for success rate (%) as a function of task difficulty (λ) the difficulty level at which the*
199 *success rate crossed 50% was considered as the critical stability point ($λ_c$), indicating the individual's skill level in task.* **B.**
200 *Correlation between the hand and cursor movement during CST.* **C.** *Sensorimotor lag between the cursor and the hand*
201 *movements.* **D.** *Ratio of hand RMS over the cursor RMS calculated for each trial, representing the gain of the response.*

Redundancy of control strategies in CST performance

203 The CST, as described earlier, affords redundancy in the control strategies that could result in task
204 success. Although covert in aggregate level of performance (i.e., **Figure 2**), single trial observations of
205 hand and cursor movements suggested that different underlying control objectives might be at play.
206 Two types of behavioral patterns appeared recognizable in the data. In one case, the cursor seemed to
207 be always balanced around the center of the screen, and any deviations from the center induced a
208 response to bring the cursor back to the center. This was reflected in the oscillatory movements of the
209 cursor around the center, shown in example trials in Figure 1B and D (first row). In other trials, the
210 cursor either exhibited a slow drift from the center or remained relatively still anywhere within the
211 boundaries of the screen, with only limited attempts to bring the cursor back to the center (for example,
212 **Figure 1**B and D, second row). We hypothesized that these patterns of behavior arise from different
213 control objectives, each focused on a different state variable in the state-space of the cursor movement.

214 In the former case, the position of the cursor appeared to be the primary control variable. Under this
215 strategy, subjects might pursue the objective of keeping the cursor near the center of the screen. We
216 refer to this strategy as the Position Control strategy. In the latter case, the cursor velocity seemed to be
217 of primary importance for control, with the objective to slow down cursor velocity regardless of its
218 position in the workspace. We refer to this strategy as the Velocity Control strategy.

219 Can we distinguish between different control strategies by examining behavior? To test this idea, we
220 took a computational approach by developing a generative model based on optimal feedback control
221 (Todorov & Jordan, 2002) that could simulate the task under different conditions and with different
222 objectives (Todorov & Jordan, 2002). The model involved a controller that generated optimal motor
223 commands based on a given strategy to perform the CST via a simple effector model. The model also
224 contained a state estimation block that estimated the states of the system based on the given feedback
225 (Todorov, 2005). In this case, cursor position and cursor velocity were used as feedback to the controller
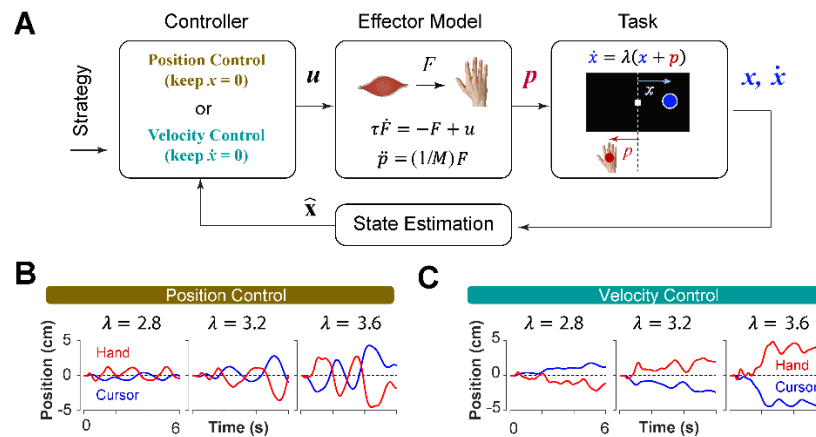226 at each time step. **Figure 3**A illustrates a block diagram of this model.

227

228 *Figure 3: A generative model to performs the CST. **A**. An optimal feedback controller generates motor commands based on two*
229 *control objectives, position and velocity control. The motor command leads the movement of the effector (hand), which*
230 *performs the CST. The cursor position and velocity are provided as feedback from which all the states are estimated and fed*
231 *back to the controller. **B** and **C**. Example trials simulated under the two control objectives for different difficulty levels: keeping*
232 *the cursor at the center (**B**; position control) and keeping the cursor still (**C**; velocity control).*

233

234 The control gains used in the controller to generate the motor commands were optimally found by
235 minimizing the sum of two cost functions: the cost of effort to reduce energy, as well as the cost of
236 accuracy that prevented the states of the system from making large deviations (2):

$$J = \sum_{t=1}^{n} \left(\mathbf{x}_t^T \mathbf{Q} \mathbf{x}_t + u_t^T R u_t \right)$$

(2)

237 where u and $\mathbf{x}$ represented the motor command and the state vector of the system, respectively. In this
238 model, the state vector consisted of six states: the position, velocity and acceleration of the hand, as
239 well as the position, velocity and acceleration of the cursor (see Methods). Variables t and n represent
240 the time, and the total number of time steps, respectively, in a trial. The matrix $\mathbf{Q}$ and the scalar R
241 determined the weight of accuracy and effort in the cost function, respectively. Importantly, the matrix
242 $\mathbf{Q}$ allowed for determining which states of the system were of primary importance in the control

243 process. Therefore, the implementation of different control objectives in the controller was done
244 through setting the Q matrix appropriately. As such, a Position Control strategy was implemented by
245 setting the weight of cursor position in the Q matrix to a large value, emphasizing the primacy of cursor
246 position as a control variable. Similarly, to implement the Velocity Control strategy, the weight of the
247 cursor velocity in the Q matrix was set to a large value (see Methods). By simulating the task for each
248 control strategy, we could generate synthetic behavior similar to that of humans and monkeys. **Figure**
249 **3**B and C illustrate a few example simulations of the task under different difficulty levels for the Position
250 Control and Velocity Control, respectively. As exemplified, the simulated trials for Position Control show
251 oscillatory movements of the cursor around the center, whereas the trials generated based on Velocity
252 Control, exhibited slow drift of the cursor from the center with minimal attempt to correct for such drift.
253 These characteristics were similar to the observed patterns of behavior in human and monkey data
254 (Figure 1B and D).

255 To further identify the behavioral signatures associated with each control objective, beyond the
256 apparent differences between single trials, we conducted a series of simulations in which the model
257 performance was examined for a range of task difficulties, and novel predictions of the model for each
258 control objective were assessed. For each control objective, the task was simulated for different
259 difficulty levels, ranging from $\lambda = 1.5$ to $\lambda = 7$, with increments of $\Delta\lambda = 0.2$. For each difficulty level,
260 500 trials were simulated (see Methods for details). In the first step, we performed the same set of
261 analyses as reported in **Figure 2** to evaluate how the model compared to human and monkey behavior
262 at an aggregate level of CST performance. **Figure 4**A illustrates the overall performance of the model for
263 both Position Control and Velocity Control strategies. As shown, for each metric, the model exhibited
264 comparable behavior to experimental data with regard to the task difficulty: the success rate dropped in
265 a sigmoidal fashion, the correlation between hand and cursor movements increased, and the response
266 lag between hand and cursor as well as the hand/cursor gain decreased. These results showed that,
267 overall, both simulated control strategies were capable of producing similar behavioral characteristics as
268 humans and monkeys. But more interestingly, despite no apparent advantage of one strategy over the
269 other in the task success (**Figure 4**A, top panel), they showed differences in the magnitude of hand-
270 cursor correlation, lag and gain. Namely, Position Control consistently showed larger magnitudes for
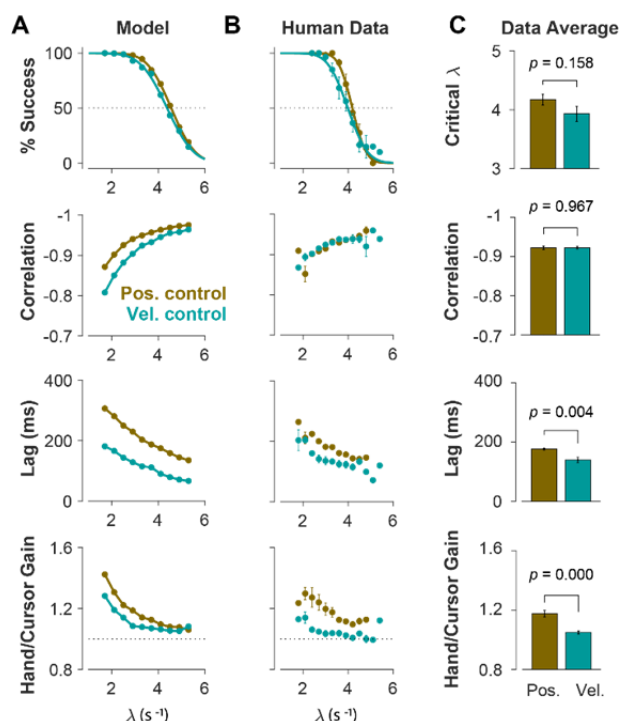271 correlation, lag, and gain for any given task difficulty.

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*Figure 4: Different control objectives result in measurably different behavior. Overall performance of the model (**A**) and human subjects (**B**) for two control objectives, Position Control and Velocity Control. The four rows show success rate (first row), correlation between hand and cursor movement (second row), sensorimotor lag between cursor and hand movements (third row), and the hand/cursor gain, defined as the RMS of hand movement over the RMS of cursor movement during each trial (last row). The error bars on the human average data indicate the standard error of the mean across subjects for each group. **C**. The average performance across difficulty levels and subjects within each group. The Critical λ (first row) indicates the difficulty level at which the success rate crosses 50%.*

Experiment 2: CST performance under explicit instructions

The model indicated that differences in behavioral metrics exist for Position vs Velocity Control. This led to a new experiment for which we recruited two new groups of human subjects (*n*=6 per group). Each group performed the CST under the same procedure as described in Experiment 1, except that this time each group was explicitly instructed to use a specific control strategy. One group was asked to perform the task with the objective of "keeping the cursor at the center of the screen at all times". This instruction was to induce a Position Control strategy. The second group was asked to "keep the cursor still anywhere within the boundaries of the screen". This instruction aimed to induce a Velocity Control strategy (see Methods for details). In each group, the kinematic behavior of hand and cursor was collected, and the control metrics were calculated. The goal was to elicit differences in performance between the two groups and, if such differences were found, determine whether they matched the behavior of the corresponding model.

The summary of performance for both human subject groups is shown in **Figure 4**B. The general trends of all four measures with respect to the task difficulty were consistent with the data generated by the model, as well as the human data from Experiment 1 (**Figure 2**). Importantly, the behavioral differences between the two control strategies in human data matched the predictions of the model relatively well (**Figure 4**A, B): the rate of success was similar, and with the exception of hand-cursor correlation, the group with Position Control instruction showed significantly larger hand-cursor lag (unpaired t-test: t_{10} =

301 3.79, p = 0.004) and hand-cursor gain (unpaired t-test: t_{10} = 5.27, $p < 10^{-3}$) compared to the group with
302 Velocity Control instructions (**Figure 4**C).

303 These results showed that the model not only captured the overall performance features observed in
304 the data, it also successfully demonstrated the redundancy of control strategies in CST performance,
305 and qualitatively distinguished between such strategies at an aggregate level of performance. To ask
306 further, can we identify, in a quantitative way, the control strategy employed by an individual, or even in
307 a given trial, when no explicit information about their preferred strategy is available? To this end, we
308 examined performance at single-trial level and introduced quantitative measures that evaluated the
309 degree to which a particular control strategy was used in that trial, as described in the next section.

Behavioral traces of control strategy in an individual's overall performance

311 To further investigate what control strategy was preferred by an individual or in a given trial, we
312 examined the predictions of the model about the cursor behavior in state space, and then tested these
313 predictions using experimental data from Experiment 2. Two metrics were defined that captured the
314 state-space behavior of the cursor in each trial. First, we examined the average cursor position and
315 cursor velocity in each trial, represented in the state space of cursor movement. This provided a single
316 data point for each trial in state space, indicating whether on average there was a drift in cursor position
317 and its velocity away from zero ($x = \dot{x} = 0$). It was expected that for Position Control, all trials scattered
318 around the origin of the state space, whereas for Velocity Control, they could deviate from the origin.
319 We also examined whether the states of the cursor correlated. **Figure 5**A illustrates the state-space
320 representation of cursor movement based on model simulations for both Position Control (top) and
321 Velocity Control (bottom), where each data point represents one simulated trial. As shown, the
322 distribution of trials in this space differed markedly between the two control objectives. The Position
323 Control strategy resulted in a distribution with little correlation between cursor position and its velocity,
324 and closely scattered around the center. In contrast, the Velocity Control strategy revealed an elongated
325 distribution with a relatively strong correlation between the cursor position and its velocity. This allowed
326 us to distinguish between different individuals' preferred control strategy.

327 To validate the model predictions, the same analysis was performed on the empirical data from
328 Experiment 2. **Figure 5**B illustrates three example subjects from Position Control and Velocity Control
329 groups, and **Figure 5**C shows a summary of how the correlation values differed across control strategies
330 for the model and the empirical data. As shown, overall, subjects in the Velocity Control group showed
331 significantly larger correlations than individuals in the Position Control group (unpaired t-test on the
332 Pearson correlation coefficient: t_{10} =4.06, p=0.002). Based on the within-group variability, this allowed
333 us to determine how pronounced a subject executed their respective strategy compared to other
334 subjects in the same group. This metric, therefore, provided a quantitative way of estimating where on
335 the spectrum of control strategy an individual's performance lies with respect to other performers.
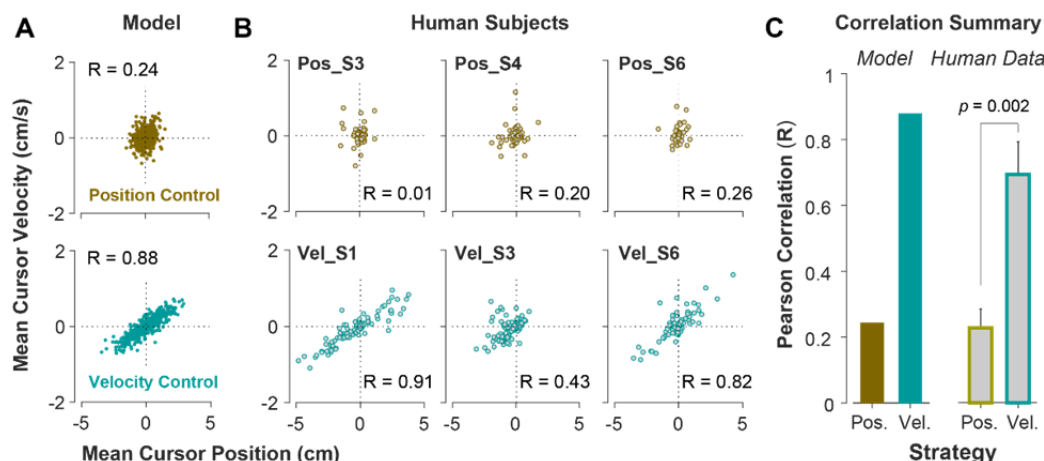
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*Figure 5: State-space distribution of trials reveals different control strategies. **A**. Mean cursor velocity plotted against mean position for each trial, shown for the position control objective (top) and velocity control objective (bottom). Each data point represents one successful trial and was simulated for a range of difficulty levels up to the critical λ value (corresponding to 50% success rate). **B**. Three example human subjects from the position control group (top row) and velocity control group (bottom row). Each data point represents one successful trial. The data represents an ensemble of trials ranging in difficulty levels up to the critical λ value for each subject. R indicates the correlation between the trial position and velocities. **C**. Pearson correlation coefficient between cursor mean position and velocity for each control objective in the model (left) and human data (right). The human data shows the mean (±SE) across subjects for each control objective group.*

The effects of control strategy at a single-trial level of behavior

Due to the task's redundancy the choice of control strategy may not be fixed for an individual throughout their performance and might vary from one trial to the next. It is therefore of great interest to determine, in a given trial, to what extent the behavior is the outcome of Position versus Velocity Control strategies. To this end, we examined the magnitude of cursor movement calculated as the root mean squared (RMS) of its position and velocity in each trial. This was directly related to the objective functions used in the model (equation(2), which provided a more direct comparison regarding the primacy of position versus velocity in the control of the cursor: a Position Control strategy aimed to minimize the RMS of cursor position, while Velocity Control aimed to minimize the RMS of cursor velocity. This distinction could be well represented in the state-space of the cursor movement.

Figure 6A illustrates the model prediction for the RMS of cursor position and cursor velocity plotted against each other for the Position Control (top) and Velocity Control (bottom). For Position Control, the distribution of trials leans towards the vertical axis (restricting cursor position but allowing large cursor velocities), whereas for Velocity Control, it leans mainly towards the horizontal axis (a larger range of cursor positions but restricted velocities). This distinction could be quantified by the slope of a fitted regression line to the data, with relatively larger slopes indicating Position Control and smaller slopes signaling Velocity Control. Similar patterns of behavior could be observed in the human data from Experiment 2 as illustrated in **Figure 6**B and C, with the Position Control group showing significantly larger regression slope than the Velocity Control group (unpaired t-test, t_{10} = 6.33, $p<0.001$). The regression slope could more clearly distinguish between individual trials than could the correlation coefficient metric shown in **Figure 5**, regarding their corresponding control strategy: if a given trial in the RMS space of the cursor movement lay below/above a certain slope threshold, its performance could be considered the result of a Velocity/Position Control strategy. We could therefore use this behavioral

369 feature to develop a classifier that inferred, with a certain level of confidence, the underlying control
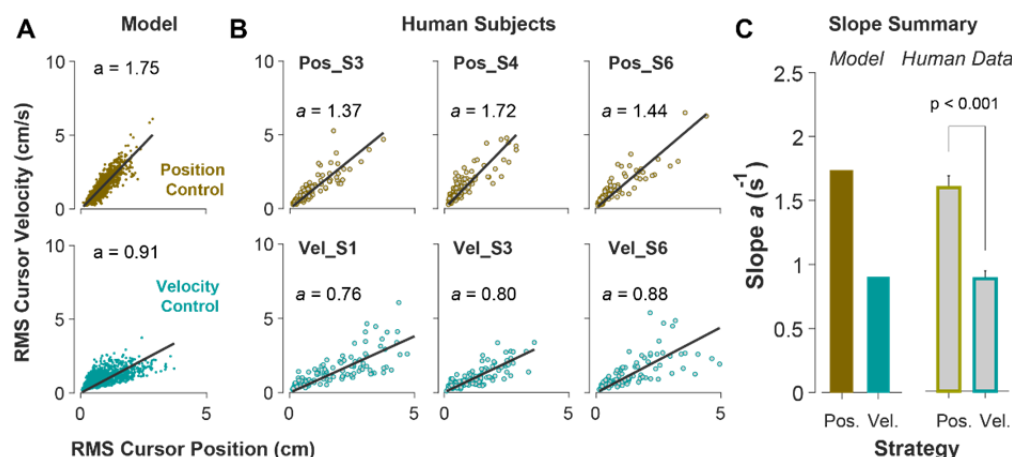370 strategy in the performance of an individual in any given trial.

371

372 *Figure 6: Identifying control strategy based on magnitude of cursor movement in the state space. **A**. Magnitude of cursor*
373 *movements quantified by the RMS of position and cursor velocity for each trial, plotted against each other; position control*
374 *objective (top) and velocity control objective (bottom). Each data point represents one successful trial and was generated based*
375 *on the model simulations for a range of difficulty levels up to the critical λ value (corresponding to 50% success rate).* ***B.***
376 *Performance of three example subjects from the position control group (top row) and velocity control group (bottom row). Each*
377 *data point represents one successful trial. The data represents an ensemble of trials ranging in difficulty level up to the critical λ*
378 *value for each subject. The values of the regression slopes are also shown.* ***C***. *Summary of the regression slopes for the RMS*
379 *plots, shown for each control objective in the model (left) and human data (right). The human data shows the mean (±SE) across*
380 *subjects for each control objective group.*

381

Inferring control strategies from behavior during CST performance

383 When monkeys performed the CST, we lacked explicit knowledge about which strategy they might have
384 employed. This is similar to Experiment 1; when humans performed the CST with no specific
385 instructions, their control objective was not explicitly available. To achieve the goal of inferring an
386 individual's control objective based on their performance, we used the control characteristics that our
387 computational approach introduced to distinguish between different control strategies. To this end, the
388 simulation results based on the cursor movement in its RMS space (**Figure 6**A) were used to train a
389 simple classifier, a support vector machine (see Methods). This classifier then determined, based on the
390 learned regression slopes from the RMS distributions (**Figure 7**A), whether a given trial was likely
391 performed under the Position Control, or Velocity Control strategy. We first tested the performance of
392 the classifier on the empirical data from Experiment 2, where the intended control strategy used by
393 each subject was known.

394 **Figure 7**B shows the cursor RMS data from three example subjects in each instructed group (similar to
395 **Figure 6**); for each trial (data point) a probability was obtained from the classifier indicating to what
396 extent a given trial was performed with the Position Control strategy (see Methods). A trial with the
397 estimated probability of >70% was considered Position Control, while a probability of <30% for a trial
398 signified Velocity Control. All other probabilities were considered as 'Uncertain' as to which of the two
399 control objectives were used. As shown in **Figure 7**B, for the Position Control group, most of the trials
400 were rightfully classified as Position Control trials, and similarly for the Velocity Control group, the
401 majority of trials were classified under Velocity Control strategy. The average probability across all trials

402   for each individual was also obtained as an overall measure of the control objective for that subject. This
403   average measure is shown in **Figure 7**B for the example subjects and summarized in **Figure 7**C for all
404   subjects in each group. This showed that the classifier correctly determined the control strategy used by
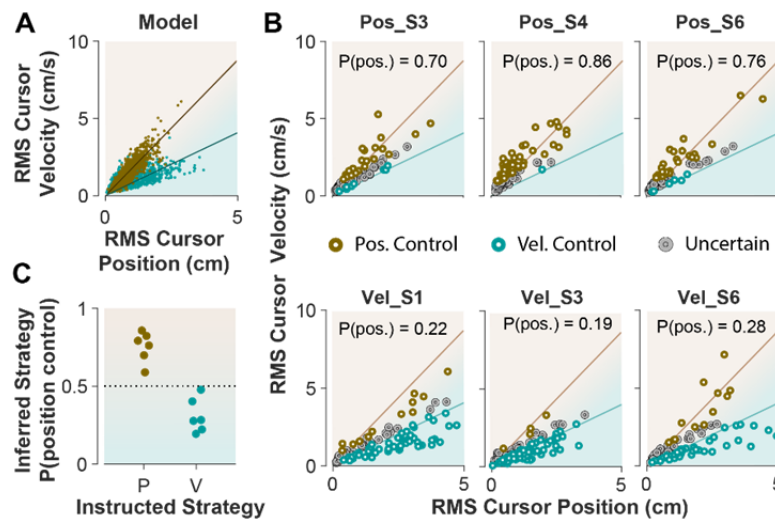405   each individual without being trained on any experimental data.

406

407

*Figure 7: Classifying control strategies in humans who received explicit instructions. A. Simulated data in the RMS space of
cursor movement used as training set for a classifier to determine the control objective of each trial. B. Data from three example
subjects in each group, where each trial was classified as position control (brown), velocity control (cyan), or uncertain as to the
control objective (grey). To obtain the control objective of each trial, the classifier (a support vector machine; see Methods)
obtained the probability of that trial performed with position control objective, where P(pos)>70% was classified as position
control, P(pos)<30% was classified as velocity control, and everything else was classified as uncertain. The average of P(pos)
across all trials for each individual is shown inside the respective plot. C. Overall probability of Position Control summarized for
all subjects instructed in the position and velocity control groups of Experiment 2.*

416   The ultimate test of our approach would be to infer the control strategy used by individuals whose
417   strategy was unknown, that is the monkeys, and humans who received no instructions about control
418   strategy in Experiment 1. After representing the performance of each subject in the RMS space, the
419   classifier was used to determine what control strategy was used in each trial. **Figure 8** illustrates the
420   classification results for human subjects who received no instructions (Experiment 1) as well as two
421   monkeys (*Monkey I* and *J* from Quick et. al. 2018). The model simulations are also provided as reference
422   in **Figure 8**A.   **Figure 8**B and C show the data from three example human subjects, as well as two
423   monkeys, in which each trial is either labelled as Position Control (brown), Velocity Control (cyan), or
424   Uncertain (grey). Two example trials, one from each inferred control strategy are also singled out from
425   each subject's performance in **Figure 8**B and C (bottom row) to show how the hand and cursor
426   movement generally behaved under each control strategy. Calculating the average probability of control
427   strategy for each individual, similar to **Figure 7**, we could infer which control strategy was of primary
428   importance for each subject (**Figure 8**D). For example, human subject NI-S2 more likely adopted a
429   Velocity control strategy, while human subject NI-S4 mainly performed the task with Position Control
430   strategy (**Figure 8**B). Similarly, *Monkey I* seemed to prefer the Velocity Control strategy, while *Monkey J*
431   most likely adopted a Position Control strategy (**Figure 8**C).

432 Ultimately, our procedure enabled us to not only infer the underlying control strategy at a single trial
433 level, but also identify which control strategy was overall preferred by humans and monkeys when no
434 explicit knowledge about their control strategy was available. These results are encouraging as they
435 constitute an important step towards bridging our findings between human and monkey research, and
436 ultimately guide neurophysiological analyses to identify the neural underpinnings of control strategy in
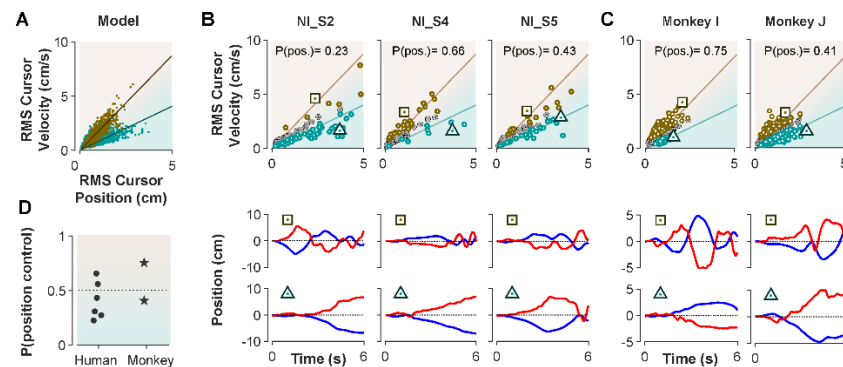437 the primates' brain.

438

439 *Figure 8: Inferring control strategies in monkeys and humans who received no instructions. A. Simulated data in the RMS*
440 *space of cursor movement was used as training set for a classifier to determine the control objective of a trial without explicit*
441 *instructions. B. Data from three example human subjects with no instructions (NI) about the control objective. Each trial (data*
442 *point) is classified based on the probability of position control, P(pos), obtained for each trial from the classifier. Trials with*
443 *P(pos)>70% and P(pos)<30% were, respectively, labeled as position control (brown) and velocity control (cyan), while other*
444 *probabilities were labeled as uncertain (grey). Two example trials, one from each control objective, are shown in the bottom*
445 *row. C. The classifier was used on data from two monkeys (Monkey I and J) who performed the CST. Similarly, trials for each*
446 *monkey were categorized as position control (brown), velocity control (cyan), or uncertain (grey). D. Overall probability of an*
447 *individual preferring the position control strategy, shown for six humans and two monkeys. This measure was obtained for each*
448 *individual as the average probability of position control across all trials.*

Discussion

450 As we seek to understand the neural basis of human motor control, it is important to build links
451 between studies in humans, where behavior can be complex and naturalistic, and monkeys, where
452 direct neural recordings are possible. Doing so requires close coordination between researchers who
453 work with humans and animals(Badre et al., 2015). With the goal to advance insights into movement
454 control, the current work developed a novel approach to parallel human-monkey behavior. In a
455 matching task design humans and monkeys performed a virtual balancing task, where they controlled an
456 unstable system using lateral movements of their right hand to keep a cursor on the screen. The task
457 was challenging and, importantly, exhibited different ways to achieve task success. The task required
458 skill, but that was conceptually simple enough for monkeys to learn the skill and ultimately achieve the
459 same level of proficiency as humans.

460 The results showed that both humans and monkeys exhibited the same behavioral characteristics as the
461 task was made progressively more difficult: success rates dropped in a sigmoidal fashion, the correlation
462 magnitude between hand and cursor increased, and the response lag from cursor movement to hand
463 response decreased. Further observations based on single trials showed that the task was possibly
464 achieved with different control strategies, both across subjects and across trials. Our goal was to identify
465 the underlying control objectives that led to different behavior, a model based on optimal feedback
466 control was developed that identified two different control objectives that successfully captured the

467   average performance features of humans and monkeys: Position Control and Velocity Control. Both
468   strategies produced behavior that was consistent with observations even at the single trial level.
469   Additional experiments revealed that humans who followed specific instructions as to performing the
470   task with Position Control ("keep the cursor at the center") or Velocity Control ("keep the cursor still")
471   matched the behavior predicted by the two simulated control policies. Model simulations exhibited
472   features that served to identify control strategies of humans and monkeys who received no specific
473   instructions at a single trial level.

474   Studies in motor neurophysiology have largely relied on simple paradigms such as center-out
475   movements (Batista et al., 1999; Cisek et al., 2003; Georgopoulos et al., 1986; Pruszynski et al., 2011;
476   Scott & Kalaska, 1997), which were brief in duration, highly stereotypical across repetitions, and could
477   be performed to a reasonable degree of success with limited sensory feedback. Such characteristics
478   were needed to make sense of noisy neural data through averaging trials over repeats of highly similar
479   behaviors. However, such tasks are not common in natural settings, where we continually utilize sensory
480   feedback to respond to our environment, interact with objects around us, and never do the same action
481   the exact same way. Indeed, such fluid, prolonged and feedback-driven interactions are what we seek to
482   understand both at the behavioral and neural levels. To this end, we need to investigate more complex
483   tasks that involve sensory-driven control and allow for different control strategies while still within a
484   sufficiently controlled scope. The task employed here, the Critical Stability Task (CST) offers advantages
485   for the study of sensorimotor control that complements previously used tasks. The task continuously
486   engages feedback-driven control mechanisms for a prolonged period of time and is rich in its trial-to-
487   trial and subject-to-subject variability. As we can titrate the difficulty of the task, both monkeys and
488   humans can learn it and we can study and model their behavior. This opens the gate towards
489   understanding the neural principles of skill learning beyond simple reaching tasks. This study showed
490   that CST afforded the examination of control strategies through a computational approach that
491   modelled monkey and human behavior in comparable fashion.

492   A critical step for bridging insights between human and monkey behavior is through the computational
493   approach that could explain behavior equally well in both human and monkey performance (Badre et
494   al., 2015; Rajalingham et al., 2022). In an earlier attempt of modeling CST, a simple PD controller with
495   delay in sensory feedback was proposed to explain the recorded behavior (Quick et al., 2018). However,
496   the model was limited in its ability to capture most features observed in the data, such as success rate,
497   or correlation between hand and cursor movements. In the past years, Optimal Feedback Control (OFC)
498   has been introduced as an effective approach to understanding the control mechanisms of reaching
499   movements at the level of behavior (Diedrichsen et al., 2010; McNamee & Wolpert, 2019; Pruszynski &
500   Scott, 2012; Scott, 2004; Todorov, 2004), separately in human research (Liu & Todorov, 2007; Nagengast
501   et al., 2010; Nashed et al., 2014; Razavian et al., 2023; Ronsse et al., 2010; Todorov, 2005; Todorov &
502   Jordan, 2002; Yeo et al., 2016) and monkey research (Benyamini & Zacksenhouse, 2015; Cross et al.,
503   2023; Kalidindi et al., 2021; Kao et al., 2021; Takei et al., 2021). Here, the OFC framework was used to
504   account for and make novel predictions about behavioral features in CST. Note that there are
505   fundamental differences between reaching and CST movements, which needed to be accounted for in
506   the modeling process. Unlike center-out reaching, the CST did not have a stationary target toward which
507   the hand needed to move; rather, it required the hand/cursor to remain anywhere within a predefined
508   area for a prolonged period of time. Also, the behavior was not tracking a point on the screen, but
509   rather moving in opposite direction of the cursor, a behavior that probably requires more cognitive

510   resources. Despite these advanced task features, OFC as a feedback control framework proved an
511   appropriate approach to examine this demanding interactive and sensory-driven task.

512   Two aspects in our computational approach are worth discussing. First, we examined control strategies
513   that only involved two main kinematic quantities of movement: cursor position and cursor velocity. One
514   might argue that other kinematic features could be explored, such as acceleration or other higher
515   derivatives of the cursor and/or the hand. However, it is important to note that, given the task of
516   keeping the cursor within a specified area for a period of time, cursor position and velocity are the most
517   directly related quantities to the goal of the task. These quantities were also less demanding to predict
518   from sensory feedback, compared to, for example, acceleration (Hwang et al., 2006; Sing et al., 2009).
519   Also note that the kinematics of the hand were not the variables of interest in the task, as the goal was
520   to control the cursor, and not the hand.

521   Second, we mainly explored Position and Velocity Control strategies separately to identify distinctive
522   behavioral features associated with each one. Experimental data, however, shows that a large number
523   of trials fall somewhere between the Position and Velocity Control boundaries (Figure 7 and 8). This
524   could be due to a mixed control strategy, where both Position and Velocity control strategies contribute
525   simultaneously to achieving the task goal, or where subjects switch strategies of their own accord. Here,
526   we aimed to determine the behavioral signatures of the extreme cases, either predominantly based on
527   position, or velocity of the cursor movement. This may increase the chance to detect differences more
528   clearly in neural activity associated with each control objective in further analysis of monkeys'
529   neurophysiological data. Even though in this experiment only a subset of trials is amenable to a clear
530   identification as using one control strategy or another, with monkeys it is possible to collect tens of
531   thousands of trials over many days accumulating enough trials for analysis.

532   Despite potential limitations, our approach was successful in two main ways. First, it provided a
533   normative explanation for the macro-level characteristics of behavior observed in human and monkey
534   data. Second, due to its generative nature, model simulations provided for not yet seen conditions and
535   made predictions about the behavior under new control objectives. In the future, our behavioral
536   analysis can serve as a foundation to classify or parse neural activity in monkeys performing complex
537   actions where trial averaging is no longer possible. This behavioral analysis holds promise to generate
538   crucial insights into neural principles of skillful manipulation, not only in monkeys but also, by induction,
539   in humans.

540   Methods

541   Participants and Ethics Statement

542   18 healthy, right-handed university students (age: 18—25 years; 8 females) with no self-reported
543   neuromuscular pathology volunteered to take part in the experiments. All participants were naïve to the
544   purpose of the experiment and provided informed written consent prior to participation. The
545   experimental paradigm and procedure were approved by the Northeastern University Institutional
546   Review Board (IRB# 22-02-15).

547   The data from two adult male Rhesus monkeys (Macaca mulatta) used in this study was taken from a
548   previously published work (Quick et al., 2018). All animal procedures were approved by the University of
549   Pittsburgh Institutional Animal Care and Use Committee, in accordance with the guidelines of the US

550   Department of Agriculture, the International Association for the Assessment and Accreditation of
551   Laboratory Animal Care, and the National Institutes of Health. For details of experimental rig and
552   procedure see the Methods in (Quick et al., 2018).

Critical Stability Task (CST)

554   The CST involved balancing an unstable cursor displayed on the screen using the movement of the hand
555   (Jex et al., 1966; Quick et al., 2014, 2018). The CST dynamics was governed by a first-order differential
556   equation as shown in equation (1). The difficulty of the task was manipulated by changing the
557   parameter λ : by increasing λ the task became more unstable, hence more difficult to accomplish. To
558   perform the task, subjects sat on a sturdy chair behind a small table, with their right hand free to move
559   above the table (**Figure 1**). A reflective marker was attached to the subject's back of the hand on the
560   third metacarpal, and the hand position was recorded using a 12-camera motion capture system at a
561   sampling rate of 250Hz (Qualisys, 5+, Goetheburg, SE). The mediolateral component of the hand
562   position was used to solve the CST dynamics with the initial condition of $x(t = 0) = 0$ (Quick et al.,
563   2018). The calculated cursor position was real-time projected as a small blue disk (diameter: 4mm,
564   approximately 0.8deg in visual angle) on a large vertical screen in front of the subject at a 150cm
565   distance. The processing delay of the visual rendering was roughly 50ms.

Experimental Design

Task

568   At the beginning of the experiment, human subjects held their right hand comfortably above the table
569   and in front of their right shoulder as shown in **Figure 1**, where the hand position was mapped to the
570   center of the screen. The visual display of the cursor and hand position was scaled such that the lateral
571   hand movements of ±10cm corresponded to ±20deg of visual angle from the screen center and served
572   as the boundaries of the workspace. Each trial started with the hand position displayed on the screen as
573   a red cursor (diameter: 4mm, or approximately 0.8deg in visual angle). Subjects were asked to bring the
574   red cursor to the center of the screen depicted by a small grey box (**Figure 1**). Once the red cursor was at
575   the center, and after a delay of 500ms, the trial started. The red cursor disappeared and a blue cursor
576   representing the x position in equation (1) appeared at the center. Subjects were instructed to keep (or
577   'balance') the blue cursor within the boundaries of the workspace for 6s for the trial to be considered
578   successful. If the cursor escaped the workspace at any time, the trial would abort and considered as
579   failed. Subjects were informed of the outcome of the trial by a message on the screen, reading "Well
580   Done!" for success, and "Failed!" for failure. The next trial started after an intertrial interval of 1000ms.
581   This feedback matched the binary reward that monkeys were given in the experiment by Quick and
582   colleagues.

Experimental Paradigm and Conditions

584   Each human subject participated in the experiment for three consecutive days. At the beginning of the
585   first day, subjects were familiarized with the experimental setup and the objectives of the task.
586   Familiarization consisted of five CST trials with moderate difficulty level. These trials were later excluded
587   from the analyses. The main experiment consisted of three main phases that were repeated on each
588   day. The first and second phases of the experiment involved 15 reaction time trials and 10 tracking trials,
589   respectively (data for reaction time and tracking trials are not reported in this study). Phase three
590   involved the CST trials, which were performed in three blocks. In Block 1, subjects performed 30 CST
591   trials, where the difficulty level was determined in each trial using an up-down method: starting from

592     $\lambda = 2.5$ in the first trial, if subjects succeeded/failed on the current trial, λ was increased/decreased by
593     $\Delta\lambda = 0.2$ in the next trial. By the end of Block 1, subjects had gradually converged to λ values in which
594   the success rate was approximately 50%. This value was considered as the critical instability value (Quick
595   et al., 2018), denoted by λ_c, and was obtained by averaging the λ's of the last 5 trials of block 1.

596   In Block 2, a stepwise increase in λ was adopted: subjects started with a difficulty level of $\lambda = 70\%\,\lambda_c$
597   (using λ_c from the previous block). They continued until they completed 10 successful trials, or 20 trials
598   in total (whichever occurred first). The difficulty level was then increased by $\Delta\lambda = 0.2$, and the
599   procedure repeated. This incremental increase of λ continued until the subjects' success rate for the
600   ongoing λ dropped below 10% (i.e., less than 2 successful trials out of 20). This marked the end of the
601   second block. In total, subjects performed approximately 120-200 trials in Block 2, depending on the
602   individual's performance.

603   In Block 3, subjects performed the CST under three selected difficulty levels of easy, medium, and hard,
604   with 20 trials for each difficulty level. These levels corresponded to λ values that led to 75% success rate
605   (easy), 50% success rate (medium) and 25% success rate (hard) obtained from each individual's
606   performance in Block 2. The exact values of $\lambda_{75\%}$, $\lambda_{50\%}$, and $\lambda_{25\%}$ were calculated by fitting a
607   psychometric curve to the success rate data from Block 2 as a function of λ (see **Figure 2**). The order of
608   difficulty was pseudo-randomly selected for each subject. For this study, we only analyzed the CST data
609   from Block 2 (stepwise increase in λ) as it matched the procedure used in the monkey experiment (Quick
610   et al., 2018). Subjects repeated the same experimental procedure on Day 2 and 3.

611   Three groups of human subjects participated in the experiment, where each group received different
612   instructions about the task goal. The first group was instructed to perform the CST "without failing to
613   the best of their ability" (no-instruction group); the second group was instructed to "keep the cursor at
614   the center of the screen at all times" (Position Control group); and the third group was instructed to
615   "keep the cursor still anywhere within the bounds of the screen" (velocity control group).

616   ## Analysis
617   To evaluate the overall performance of humans and monkeys during the CST, four quantities were
618   calculated: success rate, hand-cursor correlation, hand-cursor lag, and hand/cursor gain. For each
619   individual, the quantities were calculated as the average across trials for each bin of λ values (bin size:
620   0.3, starting from $\lambda = 1.5$).

621   The success rate was obtained as the percentage of successful trials within each λ bin. A psychometric
622   curve (a Gaussian cumulative distribution function) was then fitted to the success rate data as a function
623   of λ to estimate λ_c (critical stability, where success rate was 50%):

$$\% \text{ Success} = 50\left[1 - \text{erf}\left(\frac{\lambda - \lambda_c}{\sqrt{2}\sigma}\right)\right] \qquad (3)$$

624

625   where, 'erf' indicates the error function, and σ denotes the standard deviation of the Gaussian
626   cumulative. The correlation and lag quantities (**Figure 2**, B and C) were obtained by first cross-correlating
627   the hand and cursor trajectories in each trial, and then finding the peak correlation, and the
628   corresponding lag (**Figure 2**, see also (Quick et al., 2018)). The hand/cursor gain (**Figure 2**, D) was defined

629   as the ratio of the root mean squared (RMS) value of hand position over the RMS value of the cursor
630   position in each trial.

631   Finally, to perform the classification analysis used in **Figure 7** and **Figure 8**, a Support Vector Machine
632   method was applied to learn the two-class control objective labels. In order to build and train a
633   classifier, we used 'fitcsvm.m' function in MATLAB, where synthetic data (RMS of cursor position and
634   cursor velocity) was used as training set. To classify experimental data using the trained classifier, the
635   MATLAB function 'predict.m' was used. Finally, the posterior probabilities over each classification (i.e.,
636   the confidence on classification) was calculated using the 'fitPosterior.m' function in MATLAB.
637

638   ## Optimal Feedback Control Model
639   A generative model approach was used to build control agents that performed the CST with different
640   control strategies. The model involved an optimal feedback controller that moved the hand, a point
641   mass of m=1kg, through a simple muscle-like actuator (Todorov, 2005; Todorov & Jordan, 2002).Click or
642   tap here to enter text. The muscle model was approximated by a first-order low-pass filter that
643   generated forces on the hand in the lateral direction as in equations (4) and (5):

$$\tau \dot{F} = -F + u \qquad (4)$$

$$\ddot{p} = \frac{1}{m} F \qquad (5)$$

644

645   where F is the actuator force acting on the hand, τ is the time constant of the low-pass filter, u is the
646   control input to the muscle, and $\ddot{p}$ is the second derivative of the hand position. These equations consist
647   of three states: hand position p, hand velocity $\dot{p}$ and muscle force F. Similarly, by taking first and second
648   derivatives of equation (1), three more states were added to the dynamics of the system:

$$\ddot{x} = \lambda(\dot{x} + \dot{p}) \qquad (6)$$

$$\dddot{x} = \lambda(\ddot{x} + \ddot{p}) \qquad (7)$$

649

650   By combining equations (1) and (6) and then (6) and (7), the CST equation was expanded as follows:

$$\dddot{x} = \lambda^3 x + \lambda^3 p + \lambda^2 \dot{p} + \lambda \ddot{p} \qquad (8)$$

651

652   The advantage of the higher derivatives of CST dynamics was that it made the cursor position x, cursor
653   velocity $\dot{x}$ and cursor acceleration $\ddot{x}$ available to the controller. Hence, different control strategies that
654   directly involved these states could be explored. Note that equation (8) required that the initial
655   conditions of both hand and cursor position, velocity and acceleration all satisfied equations (6) and (
656   7). The dynamics of the system could then be captured by equations (4), (5) and (8), and represented
657   by the state vector: $\mathbf{x} = [x, \dot{x}, \ddot{x}, p, \dot{p}, F]$. By adding additive signal-independent noise $\boldsymbol{\xi}_t$, as well as
658   multiplicative signal-dependent noise $\varepsilon_t C$, the full dynamics of the system could be presented in state-
659   space format:

$$\mathbf{x}_{t+1} = A\mathbf{x}_t + B(1 + \varepsilon_t C)u_t + \boldsymbol{\xi}_t \qquad (9)$$

660

661   where ε_t and $\boldsymbol{\xi}_t$ were zero-mean Gaussian noise terms, C was the signal-dependent noise scalar, and A

662   and B represent the dynamics of the system:

$$A = \begin{bmatrix} 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ \lambda^3 & 0 & 0 & \lambda^3 & \lambda^2 & \lambda \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & -1/\tau \end{bmatrix} \qquad (10)$$

$$B = [0 \quad 0 \quad 0 \quad 0 \quad 0 \quad 1/(\tau M)]^T$$

663

664   Noisy sensory feedback $\boldsymbol{y}_t$ was given as:

$$\boldsymbol{y}_t = H\boldsymbol{x}_t + \boldsymbol{\omega}_t \qquad (11)$$

665

666   where $\boldsymbol{\omega}_t$ was a zero-mean additive Gaussian noise, and matrix H determined the available sensory

667   feedback from the vector of states. For our simulations, the feedback included the cursor position x and

668   velocity $\dot{x}$, therefore, H was defined as: $H = [1,1,0,0,0,0]$. An optimal controller determined the motor

669   command u_t to minimize the cost function J as follows (Todorov, 2005):

$$u_t = argmin\ (J)$$
$$J = \sum_{t=1}^{n} \left(\mathbf{x}_t^T \boldsymbol{Q} \mathbf{x}_t + u_t^T R u_t \right) \qquad (12)$$

670

671   where n was the number of time samples throughout the movement, and $\boldsymbol{Q}$ and R determined the

672   contribution of accuracy and effort cost, respectively. In all simulations, $R = 1$. The matrix $\boldsymbol{Q}$, however,

673   was appropriately manipulated to implement different state-dependent control strategies as discussed

674   below.

675   Position Control

676   The aim of the Position Control strategy was to maintain the cursor at the center of the screen

677   throughout the trial. This was implemented by penalizing the deviation of the cursor position x from the

678   center. In this case, the matrix $\boldsymbol{Q}$ was set to $\boldsymbol{Q} = \text{diag}([q, 1, 1,1,1,1])$, where $q \gg 1$ was a constant. As

679   such, the cost of deviation from the center for the cursor position was dominant represented in the

680   value J of the cost function, making the regulation of cursor position at the center the primary goal of

681   control.

682   Velocity Control

683   The Velocity Control strategy aimed to keep the cursor still at any point within the boundaries of the

684   workspace. In this case, upon deviation of the cursor from the center, the main goal was to bring the

685   cursor to a stop regardless of the location. This was implemented through penalizing the cursor velocity

686    $\dot{x}$ by setting the matrix $\boldsymbol{Q} = \text{diag}([1, v, 1,1,1,1])$, where $v \gg 1$ was a constant.

Simulations

Given a control strategy, the model was used to generate 500 trials of CST for each level of task difficulty from $\lambda = 1.5$ to $\lambda = 7$, with increments of $\Delta\lambda = 0.2$. The parameters of the hand and the muscle model (4)(5) were fixed to $m = 1$kg and $\tau = 0.06$s. A sensory delay of 50ms was considered when simulating the task with the optimal feedback controller (Todorov, 2005). The signal-dependent noise terms were set to $\varepsilon_t \sim N(0,1)$, and $C = 1.5$. The motor noise was $\xi_t \sim N(\mathbf{0}, \mathbf{\Sigma})$, where $\mathbf{\Sigma} = 0.4\, BB^T$. For each trial, the simulation started from the initial condition of $\mathbf{x} = \mathbf{0}$, and ran for 8s. Only the first 6s of each simulation were considered in the analysis for consistency with the experimental paradigm. The success or failure in each simulated trial was decided post hoc, by determining whether the cursor position x exceeded the limits of the workspace (±10cm from the center) within the 6s duration of the trial.

Acknowledgement

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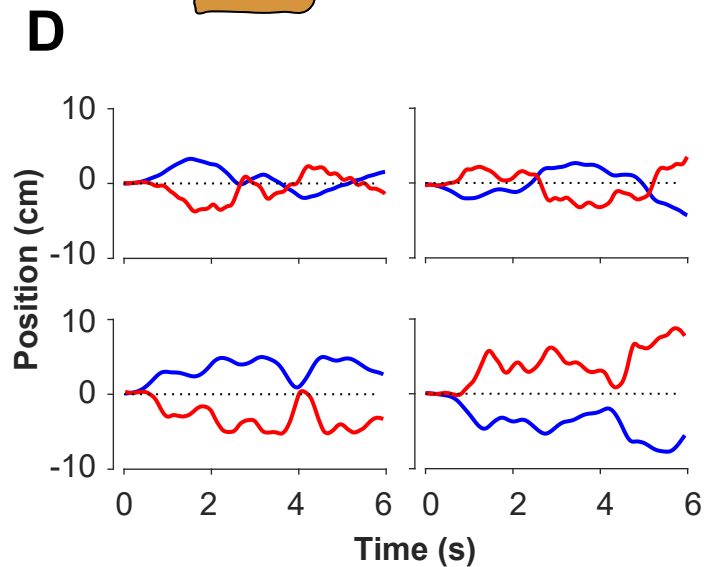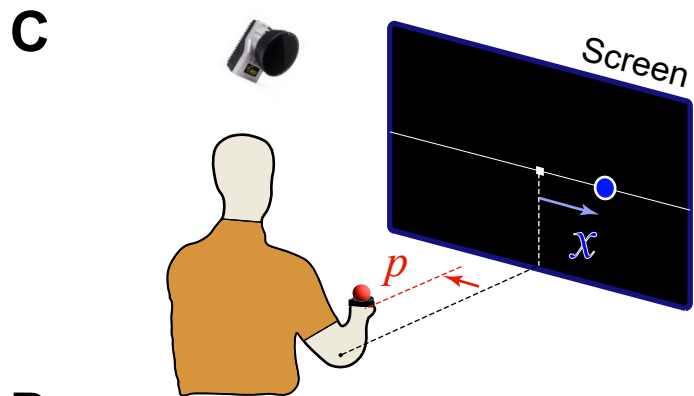782   https://doi.org/10.1109/EMBC.2014.6944152

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821

822

823

824

A

Screen

$\dot{x} = \lambda(x + p)$

B

Cursor

Hand

Position (cm)

Time (s)

C

Screen

D

Position (cm)

Time (s)

	Monkey I	Monkey J	Human #4	Human Average
A % Success				
B Correlation				
C Lag (ms)				
D Hand/Cursor Gain				

A

Controller

Position Control
(keep $x = 0$)

or

Velocity Control
(keep $\dot{x} = 0$)

Strategy

u

Effector Model

F

$\tau \dot{F} = -F + u$

$\ddot{p} = (1/M) F$

p

Task

$\dot{x} = \lambda(x + p)$

x

p

$x, \dot{x}$

$\hat{\mathbf{x}}$

State Estimation

B

Position Control

$\lambda = 2.8$ $\lambda = 3.2$ $\lambda = 3.6$

Position (cm)

Hand

Cursor

Time (s)

C

Velocity Control

$\lambda = 2.8$ $\lambda = 3.2$ $\lambda = 3.6$

Position (cm)

Hand

Cursor

Time (s)

A Model
B Human Data
C Data Average

% Success

Correlation
Pos. control
Vel. control

Lag (ms)

Hand/Cursor Gain

λ (s^{-1})

Critical λ
$p = 0.158$

Correlation
$p = 0.967$

Lag (ms)
$p = 0.004$

Hand/Cursor Gain
$p = 0.000$

Pos.   Vel.

A Model

B Human Subjects

C Correlation Summary

A Model

B Human Subjects

C Slope Summary

A Model

RMS Cursor Velocity (cm/s)

RMS Cursor Position (cm)

B

Pos_S3
P(pos.) = 0.70

Pos_S4
P(pos.) = 0.86

Pos_S6
P(pos.) = 0.76

○ Pos. Control   ○ Vel. Control   ○ Uncertain

Vel_S1
P(pos.) = 0.22

Vel_S3
P(pos.) = 0.19

Vel_S6
P(pos.) = 0.28

RMS Cursor Velocity (cm/s)

RMS Cursor Position (cm)

C

Inferred Strategy P(position control)

Instructed Strategy

P   V

A Model

RMS Cursor Velocity (cm/s)

RMS Cursor Position (cm)

B NI_S2   NI_S4   NI_S5

P(pos.)= 0.23   P(pos.)= 0.66   P(pos.)= 0.43

C Monkey I   Monkey J

P(pos.)= 0.75   P(pos.)= 0.41

○ Pos. Control   ○ Vel. Control   ○ Uncertain

D

P(position control)

Human   Monkey

Position (cm)

Time (s)