Predicting and Shaping Human-Machine Interactions in Closed-loop, Co-adaptive Neural Interfaces

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Abstract

Neural interfaces can restore or augment human sensorimotor capabilities by converting high-bandwidth biological signals into control signals for an external device via a decoder algorithm. Leveraging user and decoder adaptation to create co-adaptive interfaces presents opportunities to improve usability and personalize devices. However, we lack principled methods to model and optimize the complex two-learner dynamics that arise in co-adaptive interfaces. Here, we present new computational methods based on control theory and game theory to analyze and generate predictions for user-decoder co-adaptive outcomes in continuous interactions. We tested these computational methods using an experimental platform where human participants (N=14) learn to control a cursor using an adaptive myoelectric interface to track a target on a computer display. Our framework predicted the outcome of co-adaptive interface interactions and revealed how interface properties can shape user behavior. These findings contribute new tools to design personalized, closed-loop, co-adaptive neural interfaces.

Keywords: Co-adaptation, Game Theory, Myoelectric interfaces

1 Introduction

Neural interfaces can restore or augment human capabilities (Serruya et al, 2002; Taylor et al, 2002; Carmena et al, 2003; Hochberg et al, 2006; Pandarinath and Bensmaia, 2022; Dadarlat et al, 2023). In a neural interface, signals from the user are translated via a decoder algorithm to control a device. Decoder algorithms that adapt to users during interface operation can improve performance and enable personalization (Taylor et al, 2002; Danziger et al, 2009; DiGiovanna et al, 2009; Jarrassé et al, 2012; Orsborn et al, 2014; Shenoy and Carmena, 2014; Hahne et al, 2017; Brandman et al, 2018; Silversmith et al, 2020; Rizzoglio et al, 2021; Gigli et al, 2022; Hu et al, 2023). Users also adapt as they learn to control the interface because they receive real-time feedback (Carmena et al, 2003; Ganguly and

Carmena, 2009; Fetz, 2007; Jackson and Fetz, 2011; Albert and Shadmehr, 2016). Introducing adaptive algorithms into neural interfaces therefore creates a co-adaptive system. Prior work has demonstrated the benefits of leveraging co-adaptation to guide or assist user adaptation (Orsborn et al, 2014; Oby et al, 2019; De Santis and Mussa-Ivaldi, 2020) and maintain performance over time (Orsborn et al, 2014; Benabid et al, 2019; Silversmith et al, 2020).

However, co-adaptive systems are challenging to design because they involve dynamic, two-learner interactions: both the user and decoder may adapt simultaneously and in response to one another. Experiments have exposed the importance of identifying appropriate decoder parameters, such as the rate of decoder adaptation, to ensure stable and predictable interface control (Danziger et al, 2009; Müller et al, 2017; Madduri et al, 2022). Methods to design and analyze two-learner systems are an active area of research in neural engineering (Dangi et al, 2013; Hsieh and Shanechi, 2018) and dynamic game theory (Chasnov et al, 2020), but co-adaptive neural interfaces are largely designed and implemented empirically. Theoretically-grounded and experimentally-validated techniques to model and quantify co-adaptive dynamics will unlock new ways to design robust interfaces that harness the full potential of user and decoder adaptation.

Existing frameworks for designing co-adaptive interfaces highlight the promise of model-based approaches but either do not capture the full range of dynamic interactions that can arise between users and decoders, or do not make predictions about interaction outcomes. Past work on neural interfaces focused on the user adapting to a leading, optimal (fixed) decoder (Merel et al, 2015) or the decoder adapting to follow the user (De Santis, 2021), and most experimental neural interfaces are constrained to this limited range of co-adaptive interactions (Taylor et al, 2002; Orsborn et al, 2014; Oby et al, 2019; Silversmith et al, 2020). We instead seek methods that will be able to accommodate a wide spectrum of user-decoder interactions, where the device may shift from 'leading' to 'following' the user over time (Madduri et al, 2023). Game theory has been used to analyze the joint responses of two learners in human-human motor interactions (Braun et al, 2009; Jarrassé et al, 2012) and human-machine interactions (Müller et al, 2017; Li et al, 2019). We built on these ideas, adapting tools from control theory and game theory to create a flexible, experimentally-validated framework for analysis and synthesis of co-adaptive outcomes of continuous interactions in neural interfaces.

To build experimentally-validated frameworks for co-adaptive neural interfaces, we developed a myoelectric interface experimental platform. We found that users adapted their behavior alongside an adaptive decoder to control a cursor via their muscle activity, creating a co-adaptive system. We modeled this closed-loop system using control theory methods to quantify interactions between users and the device. This experimental platform and analysis toolkit allowed us to test analytical predictions about user-machine behaviors derived from a model treating the user and decoder as two agents in a game. Our experimental results revealed that user learning can be influenced through real-time interface adaptation and that these outcomes can be predicted using game-theoretic models. Together, our findings establish new methods to analyze and synthesize co-adaptive systems that can enable next-generation approaches for designing and personalizing neural interfaces.

2 Results

With the aim of developing computational frameworks for measuring and shaping co-adaptive interactions, we started by creating an experimental platform to study co-adaptation using non-invasive myoelectric interfaces. This platform created novel human-machine interactions for our human participants (N=14) which let us systematically manipulate decoder properties to investigate the effect of decoder adaptation on user learning. Our myoelectric interface had similar properties to many common motor neural interfaces, including brain-computer interfaces: it used high-dimensional biosignals to control a lower-dimensional movement (Seo et al, 2022; Portnova-Fahreeva et al, 2023) and was a closed-loop system that can facilitate user adaptation (Hahne et al, 2017). We then leveraged control theory and game theory to develop computational methods that can measure and predict co-adaptive outcomes. We then used our experimental platform to validate these methods by manipulating decoder adaptation parameters and demonstrating that our framework could predict co-adaptive interactions.

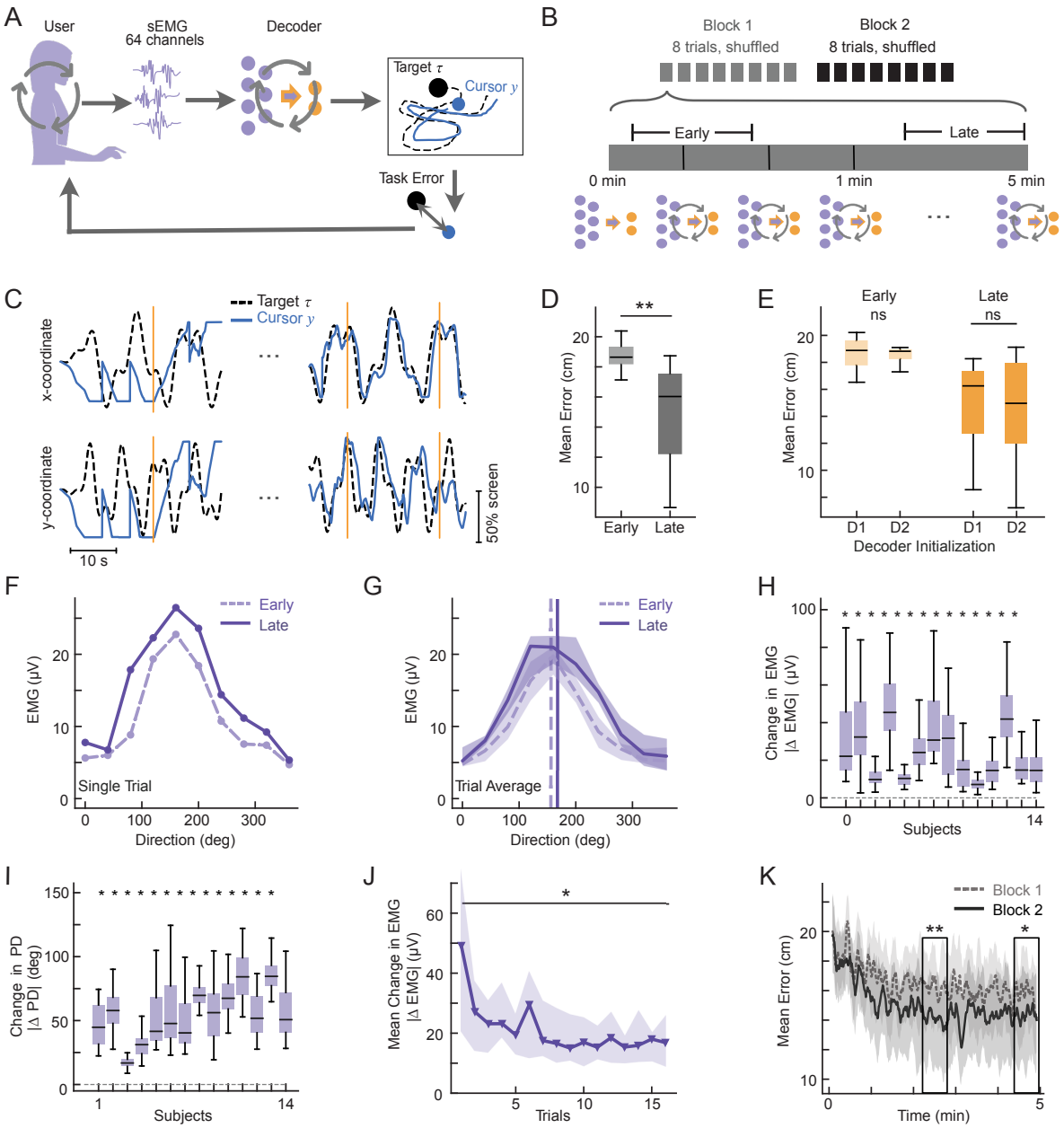

Fig. 1 Co-adaptation in myoelectric interfaces. A. Experiment schematic. Users track a target by controlling 2D cursor velocity with their muscle activity via an adaptive decoder. **B.** Experimental session schematic. Participants completed eight trials with different decoder conditions in both block 1 and 2 (random order). Each trial was 5 minutes. The decoder was initialized randomly and adapted every 20 seconds within trials. **C.** Example cursor (solid blue) and target (dashed black) trajectories. Vertical orange lines represent decoder updates. **D.** Mean error (N = 14, median with shading indicating interquartile range) early (first 30 sec) and late (last 30 sec) in trials. Error ($\|\tau - y\|$) was averaged across trials for each participant. Wilcoxon signed-rank test, **p < 0.001. **E.** Mean error (N = 14, median with shading indicating interquartile range) separated by decoder initialization (D1, D2) early and late in trials. Error ($\|\tau - y\|$) was averaged across trials for each participant. Wilcoxon signed-rank test, ns > 0.05. **F.** EMG tuning curve for one EMG channel early (dashed light purple) and late (solid purple) within a single trial. **G.** Average EMG tuning curve for one channel early (dashed light purple) and late (solid purple) across all trials (N = 16, median with shading indicating interquartile range). Preferred directions for each curve shown with vertical lines. **H.** Norm difference of the average early versus late EMG tuning curves($\|\Delta EMG\| = \|EMG(late) - EMG(early)\|$) compared to difference of zero (dashed gray) for all channels, computed for each subject (N = 63, median with shading indicating interquartile range. Wilcoxon signed-rank test with a Bonferroni correction of n = 14; *p < 0.001 for all subjects). **I.** Magnitude of angular change in EMG preferred direction early versus late ($\|\Delta PD\| = \|PD(late) - PD(early)\|$) compared to difference of zero (dashed gray) for all channels, computed for each subject (N = 63, median with shading indicating interquartile range. Wilcoxon signed-rank test with a Bonferroni correction; *p < 0.001 for all subjects). **J.** Average change in EMG tuning curves within a trial ($\|\Delta EMG\| = \|EMG(late) - EMG(early)\|$) for all subjects as a function of trial number (N = 14, median with shading indicating interquartile range). Average change in EMG of first trial is compared to last trial (Wilcoxon signed-rank test, *p < 0.05). **K.** Average error as a function of trial time in block 1 (dashed gray) and block 2 (solid black) (N = 14, median with shading indicating interquartile range). Black boxes represent comparisons of mid-trial and end-of-trial task error between block 1 and block 2 (Wilcoxon signed-rank test, **p < 0.001, *p < 0.05)

2.1 An adaptive myoelectric interface created a co-adaptive experimental platform

Participants completed a 2D trajectory-tracking task using a 64-channel adaptive myoelectric interface (Fig. 1A, Supplementary Fig. 1A). The task was chosen for its advantages in analyzing user sensorimotor transforms (Yamagami et al, 2020; Yang et al, 2021). Participants controlled a cursor using surface electromyography (sEMG) signals measured from their dominant forearm via a velocity-controlled Wiener filter decoder (see Methods). The decoder was randomly initialized at the start of every trial and then updated online every 20 seconds using previously-developed adaptive decoding algorithms (Orsborn et al, 2012, SmootBatch). Decoder adaptation conditions varied from trial to trial, and participants completed a total of 16 5-minute trials (Fig. 1B, see Methods). Performance improved as the decoder adapted during a trial (Wilcoxon signed-rank test, $p < 0.001$) (Fig. 1C, D) and these performance improvements were not impacted by decoder initialization (Wilcoxon signed-rank test, $p > 0.05$) (Fig. 1E), similar to invasive brain-computer interface adaptive decoder studies (Gilja et al, 2012; Orsborn et al, 2012; Dangi et al, 2013).

System-level performance metrics alone cannot separate the effect of user adaptation from that of decoder adaptation because performance changes could be attributed to either learner. The decoder adapted during the trial by design, leading to shifts in the D matrix according to prescribed cost functions (e.g., Fig. 5C, also reported in preliminary studies in Madduri et al (2022)). To determine whether this was a co-adaptive interface, we examined whether users adapted during each trial. We asked whether the user's behavior changed while controlling the interface by estimating the relationship between user sEMG activity and the direction of intended movement – i.e., an EMG tuning curve (Georgopoulos et al, 1986; Radhakrishnan et al, 2008; Couraud et al, 2018) (see Methods). EMG tuning curves from a sample participant revealed within-trial changes in user behavior (Fig. 1F, G). We saw similar changes in other participants (Supplementary Fig. 2). We quantified within-trial changes for each participant by calculating the magnitude of the difference between EMG tuning curves (Fig. 1H) and angular differences in the preferred direction (Fig. 1I) for the first versus last 30 seconds in the trial across all electrodes (see Methods). All participants showed significant changes in the magnitude and tuning angles of EMG activity over the course of the trial, suggesting that users adapted their behavior during the 5-minute trial (Wilcoxon signed-rank test with a Bonferroni correction of $n = 14$, $p < 0.001$) (Fig 2).

Interestingly, we observed that within-trial differences in EMG tuning curves decreased as trials progressed (Fig. 1J), demonstrating that users also adapted across the duration of the experimental session. We hypothesized that these longer timescale changes reflected users acquiring useful strategies for the myoelectric interface during the experiment. This suggests that performance may improve over time, regardless of the decoder. We tested this prediction by comparing performance in the first and second blocks, which contained trials with matched decoder adaptation conditions. We indeed saw that participants' average mid-trial and final task error was lower in block 2 compared to block 1 (Wilcoxon signed-rank test, $p < 0.05$), suggesting that task performance trajectories improved more and more quickly in block 2 than in block 1 (Fig. 1K). Taken together, these results suggest that users adapt alongside the decoder in our myoelectric interface, both within and across trials.

2.2 Co-adaptation outcomes matched control-theory predictions

Distinguishing user and decoder contributions to an interface is key to understanding and designing closed-loop, co-adaptive systems. While decoders are known exactly, the user model must be estimated. The direction-tuning analysis we used above can characterize user activity but does not provide a model for the user and, therefore, limits our ability to examine user-decoder interactions. We used methods from control theory, a discipline focused on analysis and synthesis of feedback systems, to model the behavior of users and the closed-loop system. Prior work shows that control theory can estimate changes in user trajectory-tracking behavior by separating their feedback and feedforward controllers (McRuer and Jex, 1967; Drop et al, 2013; Zhang et al, 2018; Yamagami et al, 2020). We extended these techniques to our multi-input, multi-output system to analyze co-adaptive outcomes.

We define our model of the user's encoder as the closed-loop mapping between task information and EMG activity in our myoelectric interface (Fig. 2A). Our encoder model, $E \in \mathbb{R}^{64\times 8}$, considers feedforward and feedback inputs to the user, which are derived from closed-loop task information presented to the

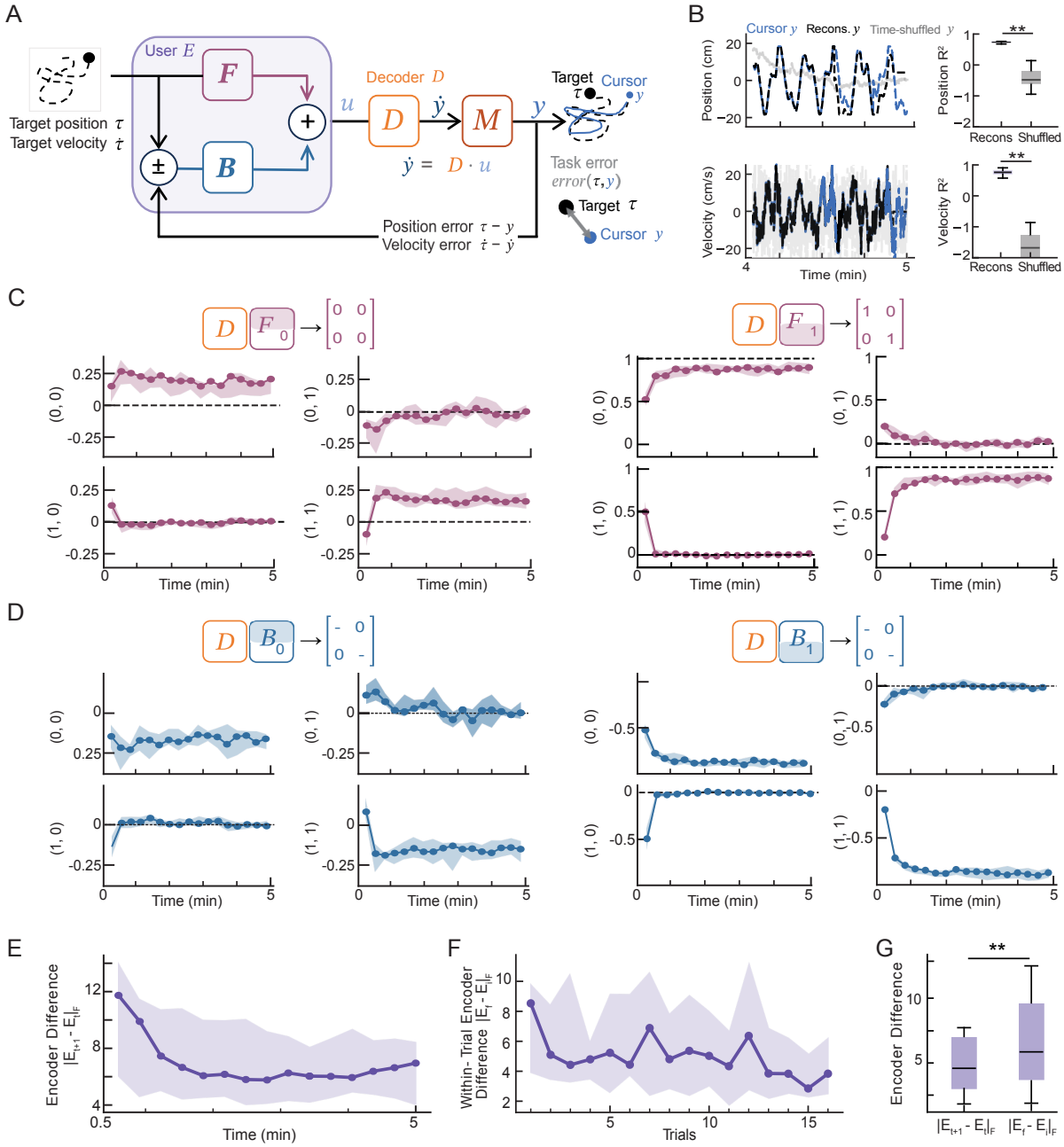

Fig. 2 Control-theoretic analysis allows for user encoder estimation and decoder-encoder analysis. A. Block diagram model of closed-loop system. The user's Encoder E outputs myoelectric activity u to the decoder D to follow the target's position and velocity. The decoder outputs velocity, which is then integrated by system dynamics M to generate a cursor position. The user sees their cursor moving with some velocity $\dot{y}$ to position y. Error in the cursor position and velocity (relative to the target) acts as closed-loop feedback to the user. **B.** Example reconstructions of cursor position (top) and velocity (bottom) from encoder estimations (dashed black), compared to the actual position and velocity (dashed blue) with a time-shuffled baseline (solid gray). Distributions of average R^2 values between actual and reconstructed position (top right) and velocity (bottom right) for actual data versus time-shuffled controls (N = 14, median with interquartile range; Wilcoxon signed-rank test, **p < 0.001). **C.** Product of the decoder matrix with feedforward contributions of the encoder matrix (N = 14, median with shading indicating interquartile range). Black dashed lines represent values that yield perfect trajectory tracking. **D.** Product of the decoder matrix with feedback contributions of the encoder matrix (N = 14, median with shading indicating interquartile range). Black dashed lines represent values that yield closed-loop stability. **E.** Average change (norm difference) in consecutive encoders ($\|E_{t+1} - E_t\|$) over the course of a trial (N = 14, median with shading indicating interquartile range) **F.** Average change (norm difference) in the initial versus final encoder within a trial ($\|E_f - E_i\|$) as a function of trial number (N = 14, median with shading indicating interquartile range). **G.** Average change in encoders (norm difference) across a full trial ($\|E_f - E_i\|$) and consecutive encoders in a trial ($\|E_{t+1} - E_t\|$) (N = 14, median with interquartile range; Wilcoxon signed-rank test; **p < 0.001).

user - target position ($\tau \in \mathbb{R}^2$), target velocity ($\dot{\tau} \in \mathbb{R}^2$), position error ($\tau - y \in \mathbb{R}^2$) and velocity error ($\dot{\tau} - \dot{y} \in \mathbb{R}^2$). We formulate an encoder model with these feedforward and feedback elements that depend linearly on target position, cursor error, and an offset β (to capture resting activity):

$$u = E \cdot \begin{bmatrix} \tau \\ \dot{\tau} \\ \tau - y \\ \dot{\tau} - \dot{y} \end{bmatrix} + \beta \cdot 1_t^\top, \tag{1}$$

where $1_t^\top = \begin{bmatrix} 1 & 1 & \cdots & 1 \end{bmatrix} \in \mathbb{R}^{1 \times t}$, and t indicates time.

The encoder matrix has both feedforward (F) and feedback (B) components:

$$E = \begin{bmatrix} F_0 & F_1 & B_0 & B_1 \end{bmatrix} \tag{2}$$

such that each component of task information, τ, $\dot{\tau}$, $\tau - y$, $\dot{\tau} - \dot{y}$, respectively corresponds with an element of the encoder, $F_0 \in \mathbb{R}^{64 \times 2}$, $F_1 \in \mathbb{R}^{64 \times 2}$, $B_0 \in \mathbb{R}^{64 \times 2}$, $B_1 \in \mathbb{R}^{64 \times 2}$. The subscripts 0 and 1 represent the 0th- and 1st-order dynamics of position and velocity, respectively. The output of the encoder is an EMG activity time series $u \in \mathbb{R}^{64 \times t}$ which is input to the decoder, $D \in \mathbb{R}^{2 \times 64}$. The decoder outputs a cursor velocity, which is integrated by the system dynamics M to a cursor position y. We estimated the user's encoders $E \in \mathbb{R}^{64 \times 8}$ within a trial with linear regression using 20 second batches of data, corresponding to the time intervals where the decoder was held constant (see Methods). This model appeared to capture useful aspects of user behavior, yielding reconstructed cursor position and velocity trajectories that were correlated with the actual cursor movements (Fig. 2B).

We then used our encoder model to quantify decoder-encoder interactions and analyze performance of the closed-loop system. One common challenge in co-adaptive systems is convergence to a stable solution or performance (Dangi et al, 2013; Müller et al, 2017; Hsieh and Shanechi, 2018). Our performance-based analysis above suggested that our co-adaptive interface may have converged (Fig 1B), but does not prove stability nor ideal performance. We exploited the separation of the feedforward and feedback pathways in our encoder model to empirically measure the stability and tracking error properties of the closed-loop encoder-decoder system. Perfect trajectory tracking is obtained when the user's feedforward input F becomes the pseudo-inverse of the decoder D and system dynamics M, which results in the following conditions: $D \cdot F_0 = 0 \cdot \mathbb{I}$ and $D \cdot F_1 = s \cdot \mathbb{I}$, where s is the frequency-domain Laplace variable. (See Methods for derivation). We used the known decoder values and estimated user encoders to quantify these values in our experimental data, which revealed that $D \cdot F_0$ and $D \cdot F_1$ approach the analytically-ideal values on average across all trials (Fig 2C). Similarly, closed-loop stability can be achieved if the feedback components of the decoder-encoder product ($D \cdot B_0$ and $D \cdot B_1$) are negative-definite diagonal matrices (Åström and Murray, 2008, Chapter 5), which was also observed in our experimental data (Fig. 2D).

We also used our encoder estimation model to revisit user learning-related changes in experiments. We observed that the change in user encoders between the start and end of a trial decreased through the trial (Fig. 2E), suggesting encoders converge within a trial. Furthermore, the within-trial change in user encoders decreased across sequential trials (Fig. 2F), mirroring our EMG analysis showing that user strategies stabilize through the course of the experiment (Fig. 1J). We found that the change in user encoders between the start and end of a trial was significantly larger than the change in sequential pairs of encoder estimates (Wilcoxon signed-rank test, $p < 0.001$) (Fig. 2G), consistent with a directed change over the course of an experiment (see Methods). Our models therefore revealed evidence of co-adaptation between the encoder and decoder that was consistent with our EMG-based analyses. By modeling the user, our control-theoretic encoder model allowed us to more precisely resolve user-decoder interactions within the closed-loop, co-adaptive interface.

2.3 Game theory model generated predictions for co-adaptation outcomes

Having established an experimental platform for co-adaptive interfaces and validated tools to analyze user-decoder adaptation, we next aimed to build tools to predict how users and decoders will interact. We leveraged game theory to model the co-adaptive interactions that arise between these two agents

optimizing their individual objectives (Başar and Olsder, 1999; Hespanha, J., 2017) (Fig. 3A). The two agents in our experiment—the user and decoder—co-adapt to achieve a shared goal: reduce task error. However, the user likely trades off error with effort, preferring strategies that achieve reasonable performance while reducing muscle activity (Todorov and Jordan, 2002). The decoder's adaptation algorithm was analogously designed to trade off error with the magnitude of the transformation (or gain) it defines between EMG inputs and cursor velocity outputs. We therefore defined cost functions for the user's encoder E and the decoder matrix D as a linear combination of task error $e(E, D)$ and agent effort f,

$$c_E(E, D) = e(E, D) + \lambda_E f_E, \;\; c_D(E, D) = e(E, D) + \lambda_D f_D, \tag{3}$$

where λ_E and λ_D are effort penalties. The error in our task is the mean square difference between the decoder output and the tracking error, $e(E, D) = \|D \cdot E \cdot z - (\tau - y)\|_2^2$, where $z^\top = [\tau^\top, \dot{\tau}^\top, (\tau - y)^\top, (\dot{\tau} - \dot{y})^\top]^\top$ is the encoder's input and $\|z\|_2$ is the 2-norm of the d-dimensional signal $z : [0, t] \mapsto \mathbb{R}^d$. We operationalized effort using the Frobenius norm (mean square entries) of the matrices E and D: $f_E = \|E\|_F$, $f_D = \|D\|_F$.

The structure of these cost functions define a potential game (Monderer and Shapley, 1996) (Fig. 3B), which can be analyzed in terms of a single potential function,

$$\phi(E, D) = e(E, D) + \lambda_E f_E(E) + \lambda_D f_D(D). \tag{4}$$

Using this potential function, we can characterize the existence of and convergence to stationary points (E^*, D^*) defined by the conditions $\partial_E \phi(E^*, D^*) = 0$ and $\partial_D \phi(E^*, D^*) = 0$. These game-theoretic stationary points represent joint strategies in the co-adaptive system that persist for a prolonged period of time. Such stationary points in a neural interface could correspond to stable neural representations (neural "encoding") and stable decoder parameters, which have been observed in co-adaptive BCIs (Taylor et al, 2002; Orsborn et al, 2012; Dangi et al, 2013; Orsborn et al, 2014; Silversmith et al, 2020). We model encoder and decoder adaptation in discrete time using gradient descent,

$$E^+ = E - \alpha_E \, \partial_E \phi(E, D), \;\; D^+ = D - \alpha_D \, \partial_D \phi(E, D), \tag{5}$$

where α_E and α_D are learning rates of the encoder and decoder, respectively.

The stationary points in our experiment reside in high-dimensional spaces as $E \in \mathbb{R}^{64\times 8}$ and $D \in \mathbb{R}^{2\times 64}$. To obtain analytical predictions, we simplify to a 1-dimensional task as in (Madduri et al, 2021) and focus on one element of the encoder at a time, holding all 3 others fixed. These stationary points are illustrated by phase portraits (Fig 3C), with nullclines $\partial_E \phi(E^*, D^*) = 0$ and $\partial_D \phi(E^*, D^*) = 0$ and streamlines of the 2-dimensional gradient $\partial \phi(E, D)$ also shown. The existence of the stationary points is unaffected by learning rates α_E, α_D, but these parameters determine the rate of convergence—or,

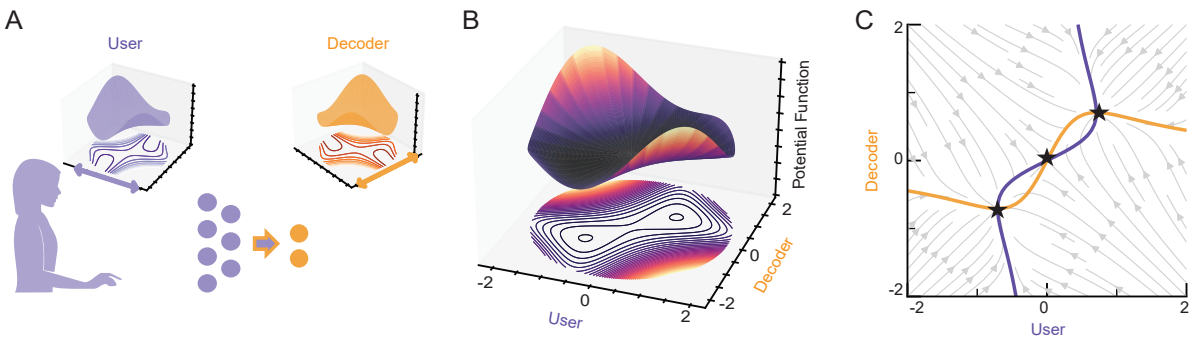

Fig. 3 Game-theoretic Model of Co-adaptive User-Machine Systems. A. Schematic of co-adaptive interfaces where the user and decoder are modeled as adapting to minimize their own individual cost functions (inset plots for each agent). **B.** Visualization of the potential function that describes dynamics within the user-decoder game model (simplified 1D user and decoder, see Methods). Two axes represent the scalar values of the user and decoder, and the vertical axis represents the value of the potential function. A 2D projection of the potential function is also shown. **C.** Gradient field of the user and decoder cost functions (with equal penalty terms, $\lambda_D = \lambda_E$). Purple (user) and orange (decoder) curves are nullclines (where the agent's gradient equals 0), which intersect at stationary points (black stars).

indeed, whether convergence occurs at all (Fig. 4A). We assessed convergence to the stationary points (E^*, D^*), where $E^* = D^* = \pm\sqrt{\frac{ab-\lambda}{a^2}}$ and a and b are both scalars corresponding to the encoder's input and task error, respectively. When $a = b = 1$, the eigenvalues of linearized dynamics at the stationary point are $\{1 - 2\alpha_E, 1 - 2\alpha_D\}$, so $0 < \alpha_E < 1$ and $0 < \alpha_D < 1$ ensures local convergence to stationarity (Strogatz, 2015, Chapter 5). Thus, the learning rates of both the user and decoder can affect convergence to stationary points and the co-adaptive system may not converge if either the learner adapts too slowly or too quickly.

The user-decoder phase portraits depend on penalty λ (Fig 5A). Indeed, altering the penalty shifts the stationary points (E^*, D^*) and, thus, affects the user and decoder efforts, f_E and f_D. To quantify this effect, we solved for the three stationary points when $\lambda = \lambda_E = \lambda_D$, finding a trivial solution at $E^* = D^* = 0$ and a mirror pair $E^* = D^* = \pm\sqrt{\frac{ab-\lambda}{a^2}}$. The trivial solution is a saddle point, whereas the mirror pairs are local minima of the agents' cost functions. Existence of multiple stationary points in the co-adaptive model suggests the same for the experimental co-adaptive system, and initialization of either agent could affect the stationary point the system converges to.

To summarize, our game-theoretic model generates the following predictions about user-decoder co-adaptation:

1. user and decoder learning rates affect convergence to stationary points ($0 < \alpha_E < 1$ and $0 < \alpha_D < 1$ is required for convergence, and the convergence rate equals $\min\{|\alpha_E - 1/2|, |\alpha_D - 1/2|\}$);
2. decoder penalty terms affect stationary points, which determine user effort ($E^* = \pm\sqrt{(ab-\lambda)/a^2}$, so larger λ yields smaller $\|E^*\|$);
3. multiple stationary points exist, so initialization of the agents affects the outcome of the interaction ($E^* = D^* = 0$ and $E^* = D^* = \pm\sqrt{(ab-\lambda)/a^2}$ are stationary).

We next used our experimental platform, where we can systematically manipulate the decoder, to test our game theoretic model's predictions for how decoder parameters (learning rate, penalty term) impact co-adaptation.

2.4 Decoder learning rates can disrupt co-adaptation

Our game-theoretic model emphasizes the importance of both the user and decoder learning rates for convergence to stationary points. One agent adapting faster than the other may limit or prevent convergence to stationarity (Fig 4A). Our model predictions echo results from previous models (Müller et al, 2017) and experimental findings from both invasive neural and non-invasive body-machine interfaces (Danziger et al, 2009; Orsborn et al, 2011). We validated our model's predictions by testing the effect of decoder learning rates in our co-adaptive myoelectric interface system. Because the user's learning rate was unknown and could not be estimated *a priori*, we varied the decoder learning rate, testing two extremes: slow and fast (see Methods). Decoders for both learning rate conditions were initialized randomly, matching all other conditions, and then adapted according to the specified cost function. Task performance was worse for co-adaptive interfaces where the decoder adapted with a fast learning rate compared to the slow learning rate throughout all trials (Fig 4B), and performance improved more within the trial in the slow condition compared to the fast condition (Wilcoxon signed-rank test, $p < 0.001$) (Fig 4C).

We found that the decoder learning rate also affected the user's encoders. We used our encoder estimates (Fig. 2) to quantify how much users' encoders changed over the course of the 5-minute trial in each decoder condition (see Methods). User encoders changed less within trials when the decoder adapted fast compared to slow (Wilcoxon signed-rank test, $p < 0.001$) (Fig. 4D), suggesting that the decoder may have adapted too fast for the user's encoder to match. We then analyzed user-decoder interactions, which confirmed that rapid decoder adaptation disrupted co-adaptation. The decoder-encoder pairs in the slow condition approached the system ideal for perfect trajectory tracking and closed-loop stability, but the fast condition decoder-encoder pairs deviated from the system ideal state in both the first-order feedforward (Fig. 4E) and feedback conditions(Fig. 4F), showing that the fast learning rate negatively

impacted the co-adaptive interactions for both trajectory tracking and closed-loop stability. Our experimental results corroborated our game-theoretic prediction that decoder learning rates will influence system behavior.

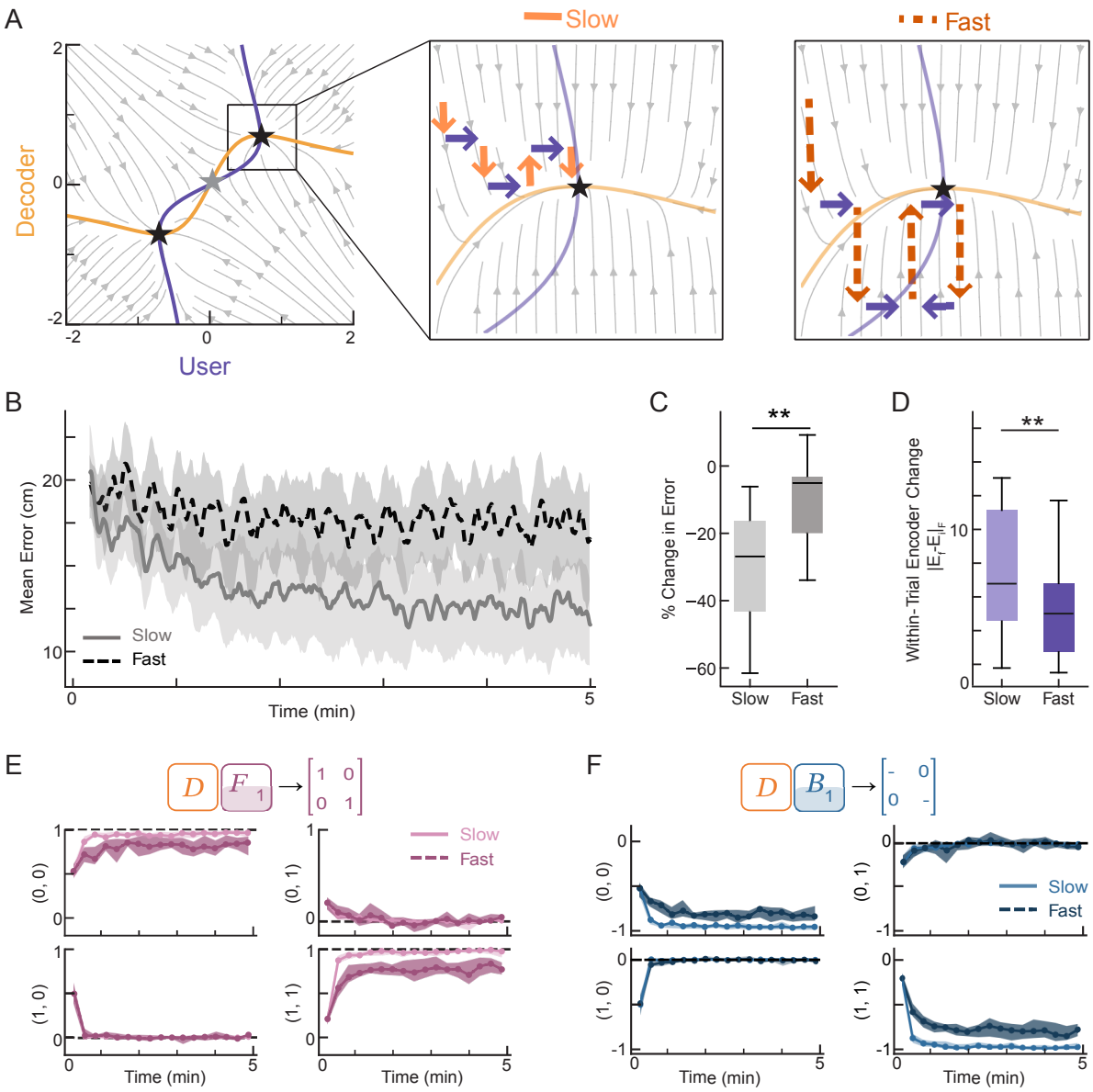

Fig. 4 Decoder learning rate influences interface performance and user learning. A. Model predictions. All panels show the gradient field of the user and decoder cost functions. Purple (user) and orange (decoder) curves show nullclines (where the agent's cost gradient equals 0) that intersect at stationary points (black stars). Slow (middle) and fast (right) panels zoom in on one stationary point and illustrate changes in the decoder (shades of orange) and encoder (purple) for different decoder learning rates. **B.** Average error as a function of time within the 5-minute trial for fast (dashed dark orange) and slow (solid light orange) decoder learning rates (N = 14, median with shading indicating the interquartile range). **C.** Percent change in error from the start of the trial (first 30 seconds) to the end of the trial (last 30 seconds), separated by fast (dashed black) and slow (solid gray) learning rates (N = 14, median with shading indicating the interquartile range; Wilcoxon signed-rank test, **p < 0.001). **D.** Average change in user's encoder within trials ($\|E_f - E_i\|$) for the slow and fast decoder learning rate conditions (N = 14, median with shading indicating the interquartile range; Wilcoxon signed-rank test, **p < 0.001). **E.** Product of the decoder matrix with first-order feedforward (F_1) contributions of the encoder matrix (N=14, median with shading indicating the interquartile range) for fast (dashed dark pink) and slow (solid light pink) decoder learning rates. Black dashed lines represent values that yield perfect trajectory tracking. **F.** Product of the decoder matrix with first-order feedback (B_1) contributions of the encoder matrix (N=14, median with shading indicating the interquartile range) for fast (dashed dark blue) and slow (solid light blue) decoder learning rates. Black dashed lines represent values that yield closed-loop stability.

2.5 Decoder "effort" penalty influenced user "effort" without changing performance

Our game-theoretic framework includes the regularization terms, $\|D\|_F$ and $\|E\|_F$, which correspond to what we refer to as "effort". Including regularization terms enforces convergence to a stable stationary (See Game Theory Methods). In the model, the scaling of the decoder regularization term, controlled by λ_D, influences the decoder effort. In turn, the user effort is also influenced by λ_D due to the linear relationship between the decoder and cursor velocity (Eq. 1). As the decoder penalty changes in our model, the stationary point and encoder effort correspondingly shift (Fig. 5A). Our model therefore predicts that changing decoder effort will not impact convergence to stationarity in the co-adaptive interface, but will influence user behavior by shifting their effort.

We tested the impact of two penalty terms – low penalty and high penalty – on decoder-encoder co-adaptation in our myoelectric interface experiments. Decoders for both penalty conditions were initialized randomly, matching all other conditions, and then adapted according to the specified cost function (see Methods). Performance was not impacted by the penalty terms (Wilcoxon signed-rank test, $p > 0.05$) (Fig. 5B), suggesting the co-adaptive systems converged similarly for both decoder conditions. Decoder effort was influenced by the penalty term as expected: higher decoder penalty resulted in decreased decoder effort (Wilcoxon signed-rank test, $p < 0.001$) (Fig. 5C). As predicted by our model, the decoder effort affected the encoder effort to reflect the trade-off in effort between the two learners. Thus, higher decoder penalty terms resulted in increases in the encoder effort (Wilcoxon signed-rank test, $p < 0.05$)(Fig. 5D). These results held regardless of the learning rate of the decoders (Supplementary Fig. 3).

While our experimental results matched model predictions, we noticed that an increase in decoder magnitude did not correspond to a similar degree of decrease in magnitude for the encoder (Fig. 5B vs. 5C). Importantly, decoder "effort" controls the magnitude of D, which defines the gain between user EMG and cursor velocity. If users do not change their effort to perfectly mirror changes in the decoder effort, the cursor's speed - an aspect of task performance not captured in our model - would change. We found that decoder penalty terms influenced the cursor speed during tracking. The lower decoder penalty term led to faster cursor speeds on average across users (Wilcoxon signed-rank test, $p < 0.001$)(Fig. 5E). Interestingly, these trade-offs differed across our participants (Fig. 5F), potentially capturing individual preferences. Our data suggest users fell into approximately three different groups: some users chose to decrease their effort and maintain a similar cursor speed, others elected to maintain a similar effort to go faster, and others changed both effort and speed to varying degrees (Fig. 5G). Our experimental results confirmed our game-theoretic model predictions and highlighted the potential of decoder adaptation to influence the user's encoder during closed-loop co-adaptation.

3 Discussion

We created novel quantitative modeling techniques to reveal how decoding algorithms can shape user adaptation in neural interfaces. The critical first step was to develop a myoelectric interface testbed that enabled systematic experiments to study how users learn to control an unfamiliar interface alongside different adaptive algorithms. Our platform provides advantages over existing human-in-the-loop simulators and related approaches, which may not fully capture how people respond to adaptive algorithms in closed-loop settings (Cheng and Sabes, 2006; Chase et al, 2009; Cunningham et al, 2011; Willett et al, 2019; Awasthi et al, 2022). We then created control theory-based estimations of user encoder transformations that allowed us to quantify critical closed-loop properties like trajectory-tracking and stability (Fig. 2C,D) and illustrated how decoder design impacted these properties (Fig. 4E,F). Prior work has shown that encoder-decoder stability likely contributes to interface performance and user learning (Orsborn et al, 2014; Taylor et al, 2002; Danziger et al, 2009), but efforts to quantify stability in adaptive neural interfaces have focused on the decoder alone (Dangi et al, 2013; Hsieh and Shanechi, 2018). By analyzing encoder-decoder pairs, we were able to characterize stability in the full co-adaptive system (Fig. 2, Fig. 4E,F) and reveal how decoding algorithms can influence user adaptation.

After developing a co-adaptive testbed and creating methods to analyze dynamic encoder-decoder interactions, we then developed a game-theoretic model to generate predictions about the behavior of different co-adaptive systems. Designing co-adaptive interfaces requires confronting a vast space of algorithm

parameters that can influence decoder and interface performance (Danziger et al, 2009; Orsborn et al,

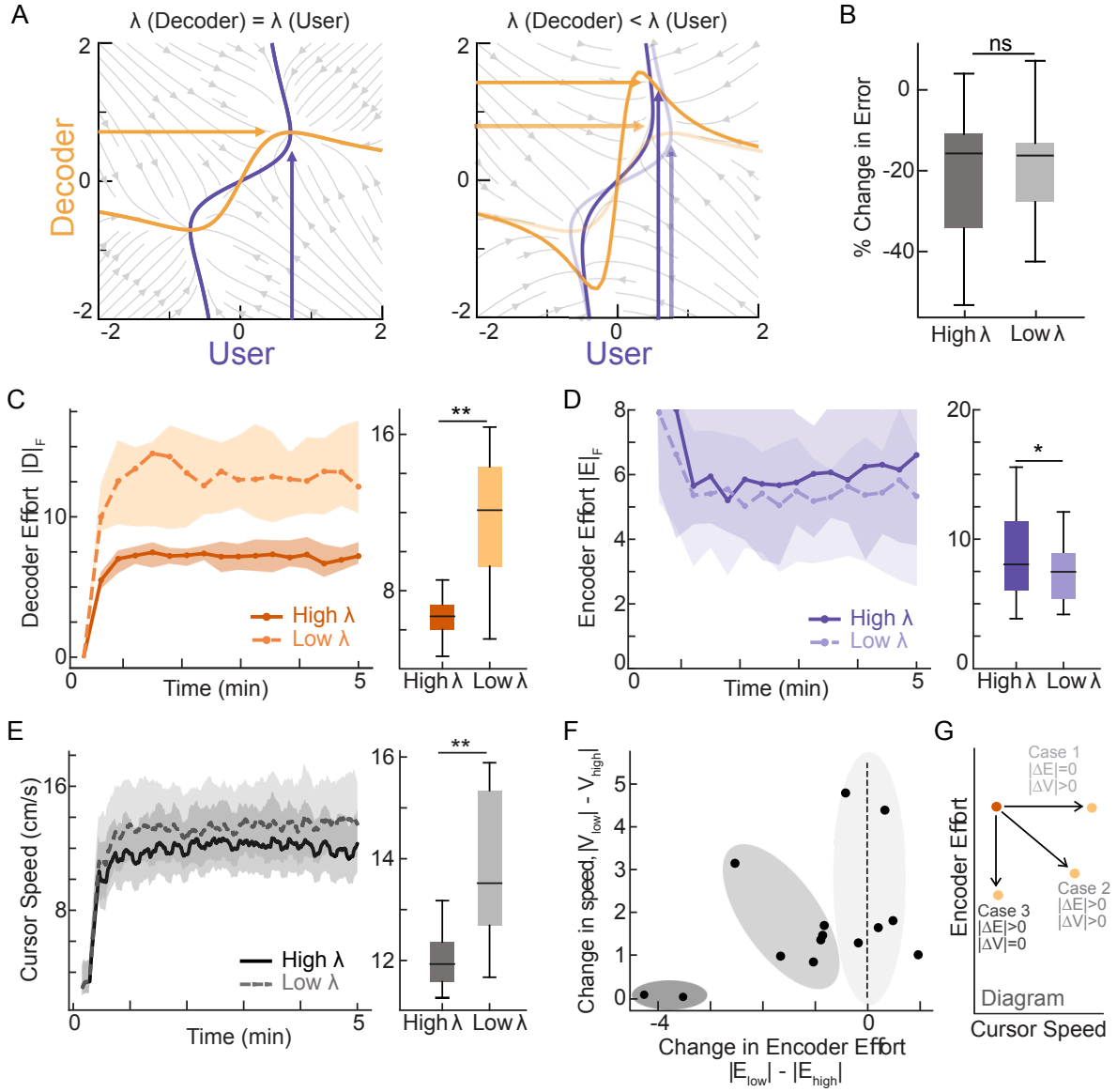

Fig. 5 Decoder penalty affects user effort and cursor velocity but not performance. A. Model predictions. Both panels show gradient fields of the user and decoder cost functions (format as in Fig. 4A) when the decoder penalty term is equal to that of the user (left) or less than that of the user (right). Arrows depict expected stationary points of user (purple) and decoder (orange). **B.** Percent change in error from the start of the trial (first 30 seconds) to the end of the trial (last 30 seconds), separated by high (dark gray) and low (light gray) decoder penalty term conditions (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, ns > 0.05). **C.** Left: Average magnitude of the decoder matrix (norm) as a function of time in the trial for low (dashed light orange) and high (solid dark orange) decoder penalty terms (N = 14, median with shaded area indicating the interquartile range). Right: Box plots are average decoder effort across the trial for each subject (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, **$p < 0.001$). **D.** Left: Average magnitude of the user encoder matrix (norm) as a function of time in the trial for low (dashed light purple) and high (solid dark purple) decoder penalty terms (N = 14, median with shaded area indicating the interquartile range). Right: Box plots are average effort for each subject across the trial (N = 14, median with shaded area indicating the interquartile range; Wilcoxon signed-rank test, *$p < 0.05$). **E.** Left: Average cursor speed as a function of time in the trial for low (dashed light gray) and high (solid dark gray) decoder penalty terms (N = 14, median with shaded area indicating the interquartile range). Right: Boxplots are average cursor speed across the trial for each subject (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, **$p < 0.001$). **F.** Average difference in cursor speed between the low and high decoder penalty conditions plotted against the average difference in encoder efforts between the low and high decoder penalty conditions for each individual participant. Shading to illustrate qualitatively identified groupings. **G.** Schematic illustrating the relationship between encoder effort and cursor speed when decoder effort changes.

2012; Dangi et al, 2013; Hahne et al, 2015; Müller et al, 2017). Our approach provides experimentally-validated methods to quantitatively model and predict outcomes of co-adaptive dynamics. These tools will enable principled interface design and optimization. For example, our framework allowed us to systematically design an interface that considers multiple objectives, balancing task error with decoder effort, which in turn influences user effort. Current neural interfaces largely aim to maximizing performance without considering potentially important aspects like user effort. Future interfaces might be designed to consider additional objectives like stability, robustness, or performance across multiple tasks. We foresee our framework becoming especially useful as the functionalities of neural interface tasks grow, where we need systematic techniques for decoder design.

Our game-theoretic model predicted the importance of decoder learning rates in co-adaptive systems. Experimentally, we found that a faster decoder learning rate yielded worse overall performance (Fig. 4C) and altered trajectory-tracking and stability in encoder-decoder pairs (Fig. 4E,F) in our myoelectric interface. Our results add to prior experimental observations from co-adaptive kinematic (Danziger et al, 2009) and brain-computer interfaces (Orsborn et al, 2011; Müller et al, 2017). Interestingly, many high-performance adaptive algorithms in invasive neural interfaces adapt rapidly (Shanechi et al, 2016; Brandman et al, 2018; Hsieh and Shanechi, 2018), whereas the fast decoder learning rate condition disrupted co-adaptive dynamics in our interface. Our model highlights that the learning rates of both the user and decoder determine system dynamics (See Section 2.3). Possibly, our naive participants may have adapted at different rates than the more experienced participants in invasive brain-computer interface studies. User learning rates may also vary across different bio-signal modalities (Jackson and Fetz, 2011). Future co-adaptive interfaces may, then, benefit from personalizing decoder learning rates based on measures of user learning rates. Methods to estimate properties of user learning, such as learning rate, in real-time will open new ways to more fully harness co-adaptation.

Our game theory model and experimental results also showed that decoder "effort" can influence user behavior (Fig. 5D). In myoelectric interfaces, this manipulation may be helpful to encourage users to learn encoders that use less muscle activity to conserve energy or to increase muscle activation for motor rehabilitation. Interestingly, we saw that users responded differently to varying decoder penalty terms, potentially reflecting personal preferences for effort versus cursor speed (Fig. 5F). Customizing interfaces based on dynamic user preferences is beneficial in human-machine interfaces like exoskeletons (Ingraham et al, 2022). Individual user preferences for cursor dynamics have also been seen in invasive neural interfaces (Willett et al, 2016). Extending our game-theoretic frameworks to include user preferences will enable design of fully personalized, custom neural interfaces, which may make these technologies more widely accessible (Yamagami et al, 2023).

Our game theory model highlighted that multiple decoder-encoder stationary points exist in neural interfaces. This raises the possibility that the initial decoder can affect the final stationary point and, in turn, the final user encoder, without significantly impacting performance (Supplementary Fig. 4A). Our experimental results confirmed that performance was not impacted by decoder initialization (Fig. 1E), consistent with prior work testing random decoder initializations in neural interfaces (Orsborn et al, 2012). While performance was not different, we found that initialization did subtly impact the stationary points as identified by the final decoder-encoder matrices (Supplementary Fig. 4E). Our findings suggested that decoder initialization might bias the encoders learned by users, which could be particularly beneficial for rehabilitation applications, which aim to shape users' behavior towards a particular goal. Our results also suggest that it may be critical to carefully consider initial training protocols for any neural interface, as it may influence user learning trajectories.

Our experiments revealed occasional deviations from model predictions, including deviations from strict encoder-decoder trade-offs (Fig. 5F) and only subtle impacts of the decoder initialization (Supplementary Fig. 4). This finding suggests that the actual user's cost might differ from our model's assumptions. For instance, our model predicts that decoder initialization would lead users to completely invert the relationship between EMG/movement and cursor velocity (Supplementary Fig. 4A), which ignores the likely possibility that users have some bias in strategies to control the interface. Additionally, there may be multiple ways to represent "effort", and these definitions may become unclear in less embodied invasive neural interfaces. Prior work has considered that users minimize effort (Flash and Hogan, 1985; Todorov and Jordan, 2002) via muscle activation (Emken et al, 2007), metabolic cost (Finley et al, 2013; McDonald et al, 2022), and motor variability (Harris and Wolpert, 1998). Studies into how users

learn to control neural interfaces suggest that other features, such as correlations between neurons, may be key factors (Sadtler et al, 2014). Deeper insights into how users learn to control different kinds of interfaces will improve our ability to model their cost functions. Alternatively, user costs may not need to be explicitly modeled. Recent work demonstrates an interface that adapts using measurements of the human's actions to steer the co-adaptive system to reach a variety of different game theory equilibria without the need to estimate or measure the human's cost (Chasnov et al, 2023). Extending such data-driven approaches to neural interfaces is a promising future direction.

By developing new computational and experimental methods to study co-adaptive systems, our results reveal how interface algorithms can influence user behavior. Specifically, our model and experimental findings show that decoder learning rate, penalty terms, and initialization influence encoder-decoder dynamics in co-adaptive interfaces. These observations are consistent with recent work suggesting that adaptive algorithms can influence neural representations learned in brain-computer interfaces (Rajeswaran et al, 2024). Our framework provides new paths to harness the complex interactions between users and algorithms in closed-loop interfaces. For example, our results hint at the possibility of designing a "curriculum" to help naive users learn to control neural interfaces, which is a task that some find challenging (Zhang et al, 2018). Decoder learning rates may need to be significantly slower early in learning when users are widely exploring strategies (Herzfeld et al, 2014; Athalye et al, 2017; Dhawale et al, 2017). Strategic decoder manipulations could be designed to bias users towards particular strategies. For example, a common aim of rehabilitation is to guide users to adopt specific actions and movements. Goal-directed decoder manipulations that encourage users to learn a particular behavior would provide a principled tool to use co-adaptive interfaces for rehabilitation (De Santis and Mussa-Ivaldi, 2020; Hung et al, 2021). We can borrow concepts from training neural networks (Bengio et al, 2009) to envision a decoder adaptation curriculum to intelligently shape user learning, fully harnessing the power of co-adaptive interfaces. Our framework provides a versatile and principled way to model and design the next generation of smart, personalized adaptive neural interfaces.

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Methods

Experimental Methods

Participants

Fourteen volunteers were recruited for this study and gave their written consent prior to experiments, according to study procedures approved by the University of Washington's Institutional Review Board (IRB #STUDY00014060). All participants were compensated monetarily for their time. All participants had no known motor disorders. Participant demographic information (including gender, weight, height, age, and handedness) was collected via a demographics survey that participants completed before the experiment (see Table 1). Only forearm circumference was measured by the experimenter, all other information was self-reported.

Table 1 Participant Demographics

	Responses
Gender	Women: 9 Men: 4 Prefer Not to Answer: 1
Weight (mean ± std, lbs.)	140 ± 21.6
Height (mean ± std, in.)	65 ± 3.4
Age (mean ± std, yrs.)	23 ± 3.9
Forearm Circumference (mean ± std, in.)	10 ± 0.8
Handedness	Right-Handed: 12 Left-Handed: 2
Level of Ambidexterity	Dominant: 8 Mostly Dominant: 5 Ambidextrous: 1

Experimental design

Participants were asked to control a cursor on the screen – using muscle activity from their forearms measured via electromyography (EMG) – to follow a 2-D continuous target trajectory as closely as possible (Supplementary Fig. 1A). Participants were told that they might not be able to control the cursor at the beginning of the trial but to expect that their cursor control would improve as the trial progressed. Participants sat in a chair with no restraints facing a computer screen (HP Compaq L2206tm, 1900 x 1600, 46.5cm x 24.5cm). The computer screen displayed a red target circle (RGB: 1, 0, 0). The cursor was a blue circle (RGB: 0, 0, 1). The target was three times the area of the cursor (Supplementary Fig 1A).The target and cursor positions were updated and displayed at 60 Hz. The task was programmed using the `pygame` and `LabGraph` Python packages.

Following prior work (Yamagami et al, 2020; Yang et al, 2021; Yamagami et al, 2021), the target traversed a pseudorandom trajectory, which was generated by a sum-of-sinusoids with randomized phases with frequencies that were prime multiples of 0.05 Hz (x-axis frequencies = 0.10 and 0.25 Hz, y-axis frequencies = 0.15 and 0.35 Hz). We randomized the phase of the sum-of-sines so that the reference trajectory would be unpredictable to the participants. Distinct prime multiples were chosen in each direction to provide separability in the x- and y-axes for any frequency-based analysis. To ensure constant signal power, the magnitude of each frequency component was normalized by the frequency squared. The trajectory was different every trial. Each trial was 5 minutes with a 5-second ramp period during which the cursor and target speed slowly increased from stationary to the experimentally-prescribed speeds. This ramp period followed prior experiments (Yamagami et al, 2021) and was added to give participants time to recognize the starting cursor and target movements. Participants completed 16 trials

of 5-minutes each in 2 blocks; each block consisted of 8 trials. Participants were given a 5-minute break in between each block but their EMG array and placement did not change throughout the experiment.

EMG signal collection and preprocessing

EMG signals were obtained using a Quattrocento system (Bioelettronica, Italy). A 64-channel high-density surface EMG electrode array (8mm inter-electrode spacing, 5x13 electrode rectangular layout) was placed on the dominant forearm of each participant, targeting the Extensor Carpi Radialis (Supplementary Fig. 1B). Electrodes were placed on the dominant arm for each participant. Once placed, the electrode array was wrapped with Coban self-adherent wrap (3M, Saint Paul, Minnesota). The electrode cables from the Quattrocento to the array were taped to minimize motion artifacts.

EMG signals were acquired using Biolite Software (Bioelecttronica, Italy) at 2048 Hz on Differential Mode with the built-in low-pass filter of 130 Hz and a high-pass filter of 10 Hz. We filtered and rectified the EMG data following prior preprocessing techniques to compute the EMG linear envelope (Yamagami et al, 2018; Chvatal and Ting, 2013). A moving average filter was applied to downsample EMG signals from 2048Hz to 60Hz (Supplementary Fig. 1C).

Myoelectric Interface Decoder

Real-time myoelectric control was implemented with a velocity-controlled Wiener filter that output a cursor velocity $v_t \in \mathbb{R}^2$,

$$v_t = D \cdot u_t \,, \tag{1}$$

where $u_t \in \mathbb{R}^N$ is the processed EMG signals of $N = 64$ channels and $D \in \mathbb{R}^{2\times N}$ is the decoder mapping. The cursor velocity is integrated to output a cursor position $y_t \in \mathbb{R}^2$,

$$y_t = y_{t-1} + v_t \Delta t \,. \tag{2}$$

where Δt is the time between cursor updates.

Myoelectric Interface Decoder Adaptation

Decoder adaptation consisted of two steps: (1) calculate the optimal decoder D^* by minimizing the cost function c_D based on the previous 20 seconds of user and trial data:

$$D^* = \min_D c_D(D) \,, \tag{3}$$

and (2) update the next decoder D following the SmoothBatch approach (Orsborn et al, 2012), which uses a weighted combination of the prior decoder D^- and the optimal decoder D^*:

$$D = \alpha D^- + (1-\alpha) D^*, \tag{4}$$

where α is the learning rate. The decoder cost function was minimized using `scipy`. To satisfy real-time timing constraints on decoder cost minimization, we initialized $D_0^* = (\tau - y) \cdot s^+$ using the previous 20 seconds of data (Madduri et al, 2022). At the start of each trial, the decoder was initialized by randomizing the decoder weightings from a uniform distribution (using `numpy.random.rand`) and multiplying by a scalar factor. Each user had two different decoder initializations, referred to as D1 and D2. Initial decoders for each participant's trial were set to D1 or D2. Note, while we programmed the decoder to update every 20 seconds, due to slight software imprecision, the decoder update actually occurred approximately every 18 seconds.

Decoder Cost

The decoder cost function was formulated in earlier work (Madduri et al, 2021) and aims to minimize both the tracking error and decoder effort as the decoder adapts. Minimizing velocity error is a common goal in user-machine interfaces, seen widely across neural interfaces (Orsborn et al, 2014; Wodlinger et al, 2014), body-machine interfaces (Seáñez and Mussa-Ivaldi, 2013), and myoelectric interfaces (Hahne et al, 2015; Radhakrishnan et al, 2008). Decoder effort is considered as part of the decoder cost since our prior theoretical analysis suggested that a regularization term in the user and decoder costs is necessary to ensure convergence in the user-decoder co-adaptation game to stable stationary points (Madduri et al, 2021).

The decoder cost c_D is constructed as a linear combination of the task *error* and decoder *effort*:

$$\text{error} = \|D \cdot u - \frac{1}{\Delta t}(\tau - y)\|_2^2 \,, \text{ effort} = \|D\|_F^2 \,; \tag{5}$$

here $\|x\|_2$ denotes the 2-norm of signal $x : [0, t] \to \mathbb{R}^d$, and $\|X\|_F$ denotes the Frobenius norm of matrix $X \in \mathbb{R}^{m \times n}$. The decoder cost c_D is then,

$$c_D = \|D \cdot u - \frac{1}{\Delta t}(\tau - y)\|_2^2 + \lambda_D \|D\|_F^2, \tag{6}$$

where λ_D is the penalty term of the decoder effort.

Decoder Conditions

We varied the decoder cost function and parameters of decoder adaptation to determine how it influenced system performance and user behavior. Specifically, we varied: (1) learning rate α, (2) decoder effort penalty term λ_D, and (3) decoder initialization. We tested two learning rates: *slow* ($\alpha = 0.75$) and *fast* ($\alpha = 0.25$), two penalty terms: *low* ($\lambda = 10^2$) and *high* ($\lambda = 10^3$), and two randomized initializations of the D decoder matrix: *positive* (matrix elements chosen uniformly at random in the range $[0, 10^{-2}]$) and *negative* (elements chosen uniformly at random in $[-10^{-2}, 0]$). We tested all combinations of learning rates, penalty terms, and initializations, leading to a total of eight different decoder conditions.

Data Analysis Methods

Performance Metrics

Our primary metric for quantifying performance was the tracking error, calculated as the Euclidean distance between the target and the cursor, $\|\tau - y\|_2$. We assessed changes in task performance within a trial by comparing the mean tracking error in the first (early) and last (late) 30 seconds of the trial (excluding ramp-up time). Because participants' proficiency in tracking varied, we quantified improvements over time by calculating the relative error: $\frac{error_{fi}}{error_i} \times 100\%$, where $\text{error}_{fi} = \text{error}_{final}$ - $\text{error}_{initial}$.

Statistical Analyses

All analyses treated participants as individual data points and computed the mean across decoder conditions (learning rate, penalty terms, initialization) and trials. To assess statistical significance across time and conditions for each participant, we used a one- or two-sided Wilcoxon signed-rank test (`scipy.stats.wilcoxon`), which is a paired, non-parametric test. We chose a non-parametric statistical test because of subject-to-subject variability. Figure boxplots were plotted with `matplotlib.pyplot.boxplot` (center line, median; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range; fliers not plotted).

EMG Analysis

To quantify the relationship between user EMG activity and cursor movement, we computed EMG direction tuning curves, a well-established analysis used for neural and myoelectric interfaces (Georgopoulos et al, 1986; Radhakrishnan et al, 2008; Couraud et al, 2018). We first down-sampled and grouped intended user cursor velocities into 10 equally-spaced directions and then fit raw EMG activity to the binned directions to form EMG tuning curves. These EMG tuning curves were created for each participant, each trial, and each EMG signal (Fig. 1E). Note, since the EMG channels are differentially-recorded, we selected 63 EMG signals for the EMG tuning analysis.

To quantify the within-trial EMG changes from early to late trial segments (Fig. 1G) we computed the norm difference between the early and late EMG tuning curves:

$$\|\Delta EMG\|_2 = \|EMG_{dir,i} - EMG_{dir,j}\|_2 \tag{7}$$

where EMG_{dir} is the average EMG activity per direction and i and j indicate time points. These early and late tuning curves were calculated by reconstructing 30 second segments of trial data that equally sampled all cursor directions. To measure how the EMG activity changed across the entire experiment per participant (Fig. 1I), we averaged the $\|\Delta EMG\|_2$ across all channels for each participant to compute a mean $\|\Delta EMG\|_2$ per participant per trial.

To find the preferred direction of the EMG activity, we performed cosine-fitting analysis (Georgopoulos et al, 1986). Specifically, average EMG activity for each intended cursor direction was modeled as:

$$EMG = B_1 cos\theta + B_2 sin\theta + B_3 \tag{8}$$

where θ represents intended cursor direction and B_1, B_2 and B_3 are model coefficients. The preferred direction (PD) is:

$$PD = arctan2(B_2/B_1). \tag{9}$$

The change between early and late preferred direction (Fig. 1h) was calculated as $|\Delta PD| = |PD_{late} - PD_{early}|$.

Encoder Estimation Methods

To model the user's transformation from task space to user signals, we estimated the user's encoder E. We constructed a u matrix of EMG signals of $t = 1200$ samples (corresponding to 20 seconds of data at 60 Hz) and a matrix from task information (target position $\tau \in \mathbb{R}^{2\times t}$, target velocity $\dot{\tau}$, position error $\tau - y$. and velocity error $\dot{\tau} - \dot{y}$),

$$u = E \cdot \begin{bmatrix} \tau \\ \dot{\tau} \\ \tau - y \\ \dot{\tau} - \dot{y} \end{bmatrix} + \beta \cdot 1_t^\top, \tag{10}$$

where $1_t^\top = \begin{bmatrix} 1 & 1 & \cdots & 1 \end{bmatrix} \in \mathbb{R}^{1\times t}$, $u \in \mathbb{R}^{N\times t}$, $E \in \mathbb{R}^{N\times f}$, N is the number of signals, d is the dimension of task information, and β is an offset factor for estimation ($\beta \in \mathbb{R}^{N\times 1}$). In this paper, $N = 64$ EMG channel inputs, $d = 8$ (target position, target velocity, position error, and velocity error for both x and y dimensions), and $t = 1200$ (20 seconds at 60 Hz sampling rate). The encoder E was estimated using linear regression (`sklearn.linearmodel.LinearRegression`) with a y-intercept offset, so there was one E estimate for each 20 seconds of data.

The encoder matrix has both feedforward (F) and feedback (B) components:

$$E = \begin{bmatrix} F_0 & F_1 & B_0 & B_1 \end{bmatrix} \tag{11}$$

such that each component of task information, τ, $\dot{\tau}$, $\tau - y$, $\dot{\tau} - \dot{y}$, respectively corresponds with an element of the encoder, $F_0 \in \mathbb{R}^{64\times 2}$, $F_1 \in \mathbb{R}^{64\times 2}$, $B_0 \in \mathbb{R}^{64\times 2}$, $B_1 \in \mathbb{R}^{64\times 2}$. The subscripts 0 and 1 represent the 0th- and 1st-order dynamics of position and velocity, respectively.

We estimated the accuracy of the myoelectric encoder model by reconstructing EMG signals from the encoder estimation and compared the coefficient of determination (R^2) for the cursor velocity and position decoded from the reconstructed EMG to the actual cursor velocity and position recorded in the trial. To establish a baseline for the predictive power of our encoder model, we also computed the accuracy of cursor velocity and position decoded from time-shuffled EMG data (Fig. 2B). The time-shuffled EMG data was created by permuting the EMG signals within each trial, so that the EMG data came from the same subject and trial but different time points.

Closed-loop Decoder-Encoder Predictions

We used control theory principles to predict relationships between elements of the encoder E and decoder D. Specifically, we regarded these as linear time-invariant (LTI) transformations and analyzed them in the frequency-domain with Laplace variable s. In the frequency-domain, the machine transformation is $M(s) = \frac{1}{s} I(s)$ where I is the *identity* transformation, that is, $I(s)$ is an identity matrix for each $s \in \mathbb{C}$.

Defining $F(s) = F_0 + s\,F_1$ as the user's *feedforward* transformation, exact tracking can occur only if

$$I = M \cdot D \cdot F = \frac{1}{s} \cdot D \cdot F_0 + D \cdot F_1, \tag{12}$$

which requires $F_0 = 0$ and $D \cdot F_1 = I$. To ensure closed-loop stability, it suffices that $D \cdot B_0$ and $D \cdot B_1$ are negative-definite diagonal matrices (Åström and Murray, 2008, Chapter 5).

Decoder-Encoder Pairs

We calculated decoder-encoder pairs by multiplying the decoder ($D \in \mathbb{R}^{2\times 64}$) at each update with the feedforward and feedback contributions to the encoder ($E \in \mathbb{R}^{64\times 8}$) at each update. Each decoder-encoder pair ($D \cdot F_0$, $D \cdot F_1$, $D \cdot B_0$, and $D \cdot B_1$) resulted in a 2×2 matrix representing the dynamics between the encoder and the decoder.

Encoder Differences

We calculated changes in encoders over time using the norm-difference of encoder matrices: $\|E_i - E_j\|_F$, where i and j indicate time points. Since we started from a decoder that was initialized with randomized weightings and resulted in poor user control, the details of the first encoder E_0 were not readily interpretable. We did not include E_0 in computing or plotting the encoder differences in Fig. 2E - G. To compute encoder changes within a trial, we calculated the difference between the final (E_f) and initial (E_i) encoders, estimated by averaging the first three and last three encoders in a trial, respectively (excluding E_0). To compare data from consecutive encoders to the average change across a full trial (Fig. 2G), we computed the consecutive encoder difference by averaging across three subsequent, non-overlapping encoders and calculating the norm difference. This method ensured that the same number of encoder data points would be compared.

Game Theory Methods

We modeled the co-adaptive system in a game theory framework involving two agents: the user and decoder. The user and decoder decision variables were the entries in the matrices E and D, respectively. Each agent was modeled as having a cost function defined by a linear combination of *task error* and *agent effort*. Agent effort was quantified using the square of the Frobenius norms of the matrices E and D. Task error was defined in cursor velocity space as the squared 2-norm of $e = D \cdot u - (\dot{\tau} - \dot{y}) = D \cdot E \cdot z - (\dot{\tau} - \dot{y})$ where

$$z = \begin{bmatrix} \tau \\ \dot{\tau} \\ \tau - y \\ \dot{\tau} - \dot{y} \end{bmatrix}. \tag{13}$$

Stationary points

To help make analysis tractable, we focused on a 1-dimensional version of the task and assumed the effort penalty was identical for the encoder and decoder:

$$c_E(E, D) = \|e(E, D)\|_2^2 + \lambda\|E\|_F^2,\ c_D(E, D) = \|e(E, D)\|_2^2 + \lambda\|D\|_F^2, \tag{14}$$

where $D \in \mathbb{R}$ and $E = [F_0, F_1, B_0, B_1] \in \mathbb{R}^{1\times 4}$. To further simplify, we analyzed the effect of varying only one variable in E while holding the others constant. For each choice of $X \in \{F_0, F_1, B_0, B_1\}$, the error term has the form $e(X, D) = D \cdot X \cdot a + b$ for some scalars a and b. We solved the nonlinear equations $\partial_X c_E(X^*, D^*) = 0$ and $\partial_D c_D(X^*, D^*) = 0$ to compute stationary points (X^*, D^*).

Convergence of gradient descent

We modeled agent adaptation using gradient descent on their individual cost function,

$$E^+ = E - \alpha_E\, c_E(E, D),\ D^+ = D - \alpha_D\, c_D(E, D), \tag{15}$$

where α_E and α_D are the agent learning rates. To assess convergence of gradient descent to stationary points, we linearize the discrete-time gradient descent dynamics and compute eigenvalues of the linearization – a sufficient condition for stability is that the magnitude of all eigenvalues is less than 1.

Data availability

All data are publicly available in a Code Ocean capsule, `DOI: 10.24433/CO.4049054.v1`

Code availability

The data and analysis scripts needed to reproduce all figures and statistical results reported in both the main paper and supplement are publicly available in a Code Ocean capsule, `DOI: 10.24433/CO.4049054.v1`

Competing Interests Statement

A.L.O. is a scientific advisor for Meta Reality Labs.

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Author Contributions

M.M.M., M.Y., S.A.B., and A.L.O., were responsible for experimental design. M.M.M, M.Y., and S.L. were responsible for experimental setup, M.M.M. and S.B. conducted the experiments, M.M.M. analyzed the experimental data and prepared figures, and M.M.M., S.A.B., and A.L.O. wrote the paper.

Supplementary Materials

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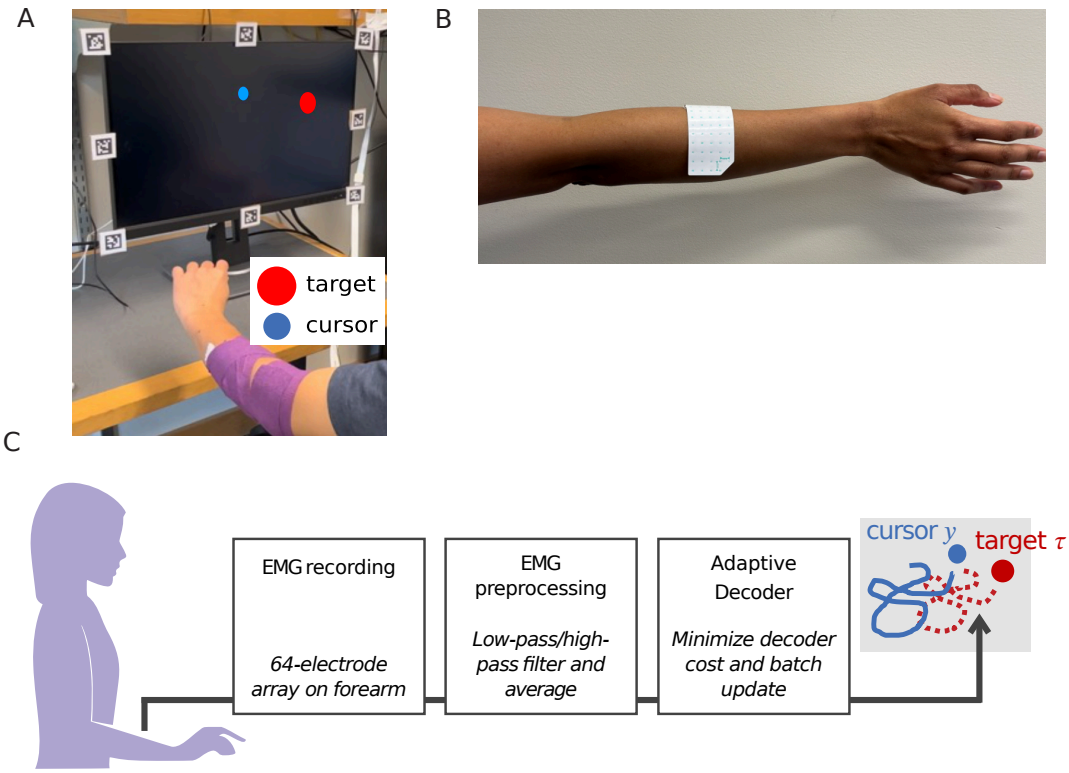
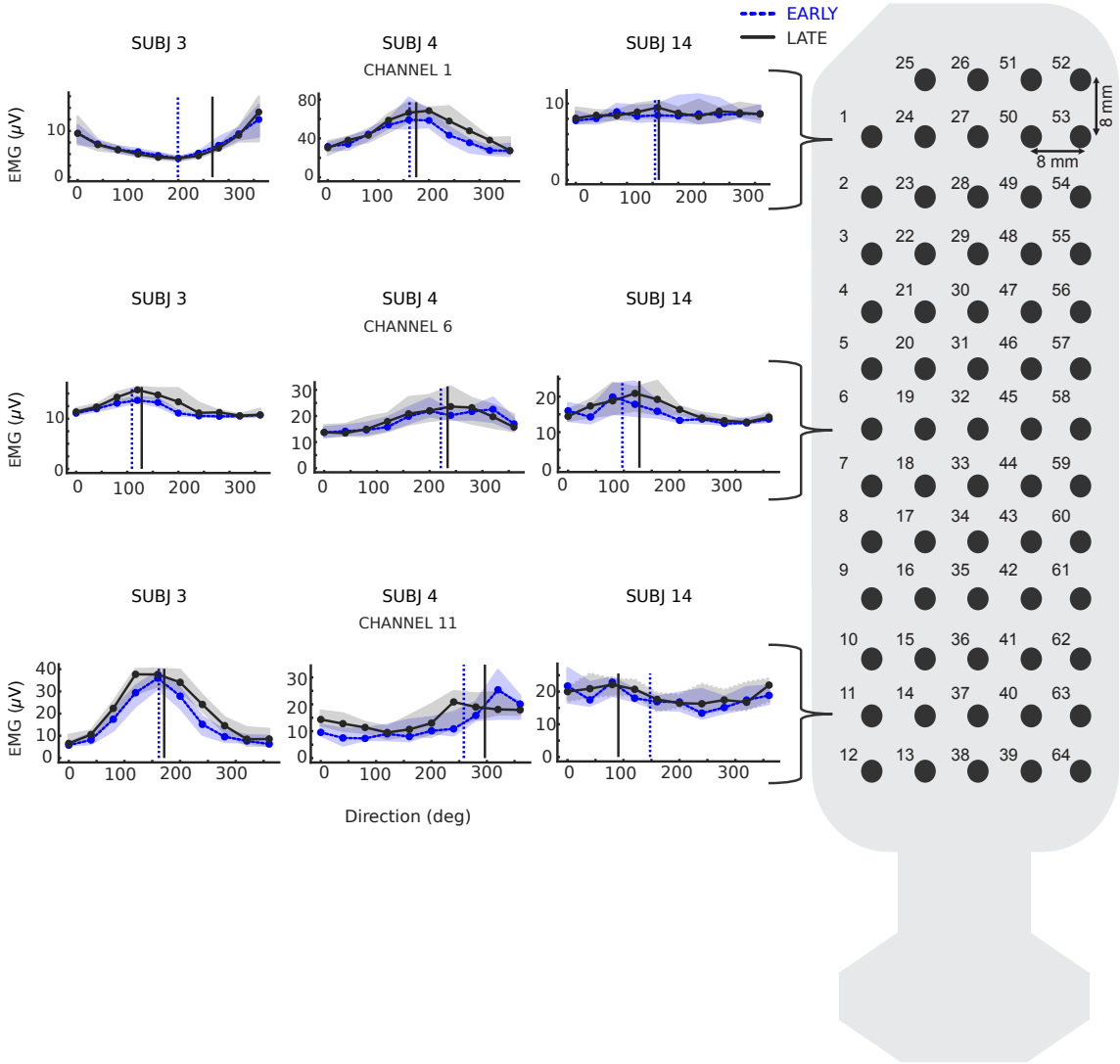
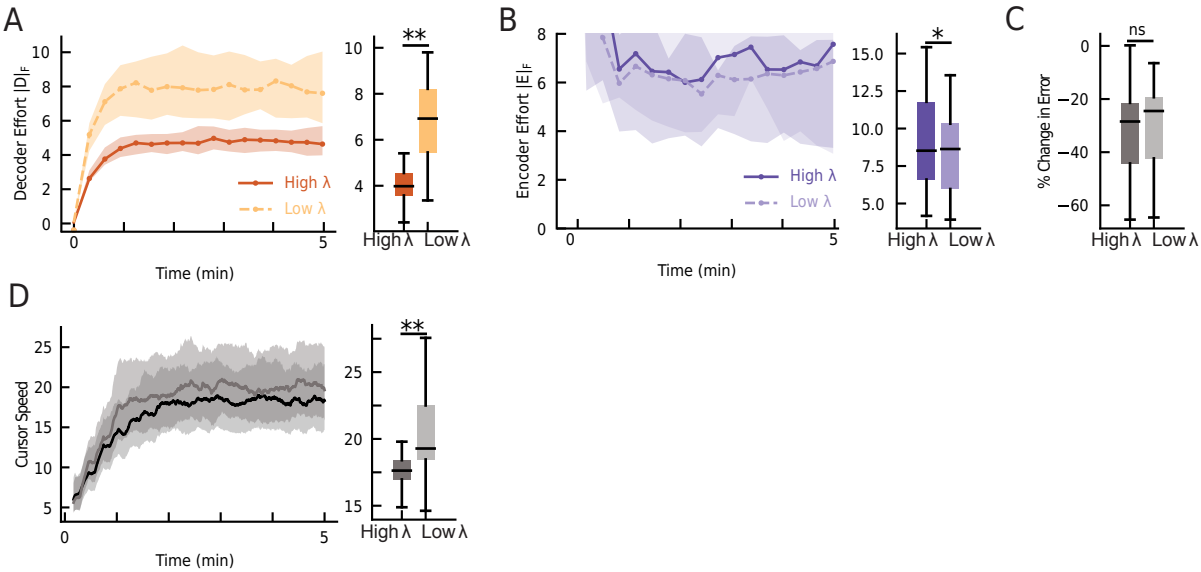


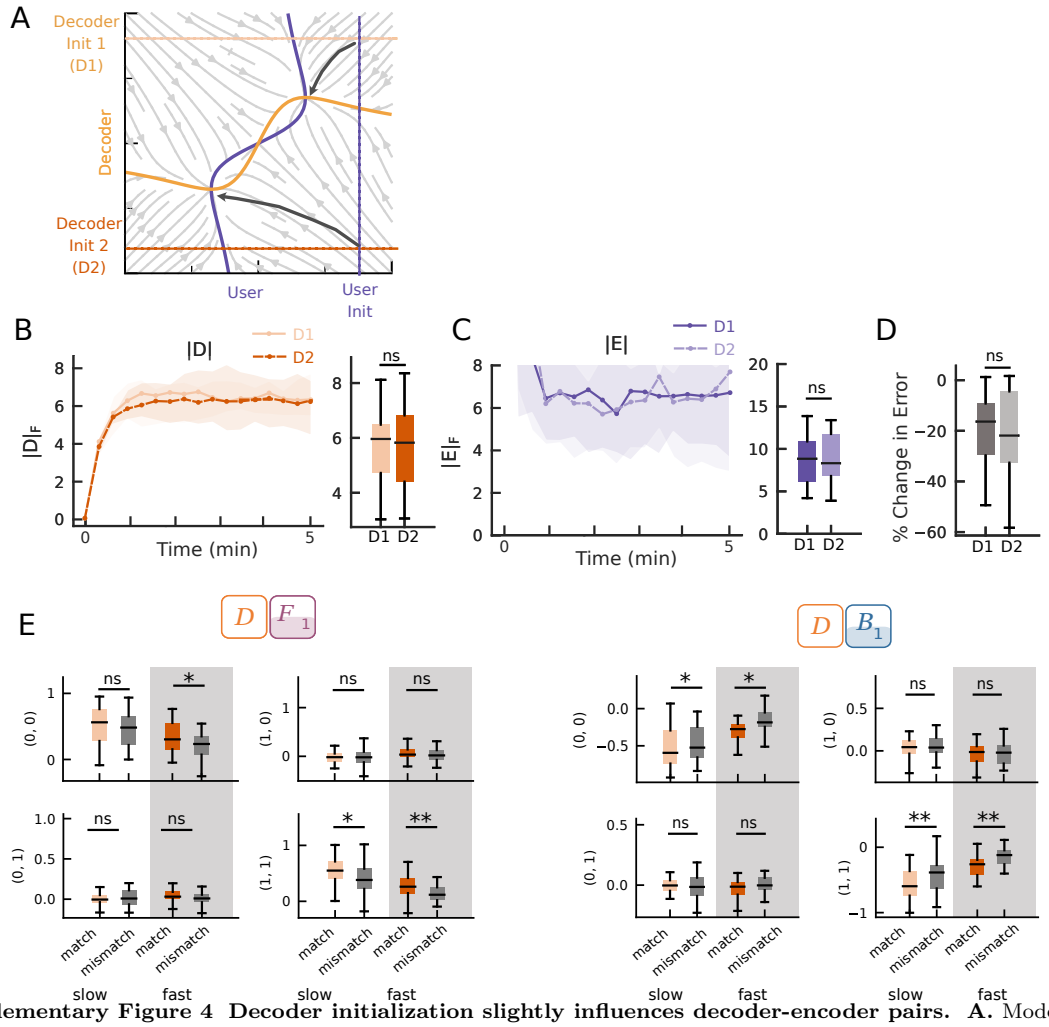
Supplementary Figure 1 Experimental testbed. A. Photograph of experiment. User tracks target (dashed red) by controlling the velocity of a 2D cursor (solid blue) with their forearm muscle activity. Muscle activity is collected via surface EMG electrodes that are placed on the participant's dominant forearm and wrapped with Coban tape. **B.** Electrode placement on dominant forearm. Surface EMG electrodes are placed on user dominant forearm to target Extensor Carpi Radialis. **C.** Schematic of EMG preprocessing and decoding pipeline. EMG signals recorded from the user forearm are preprocessed and then input to the adaptive decoder. The decoder output is the cursor velocity that is integrated to display cursor position (blue) on the screen.



Supplementary Figure 2 Surface EMG electrode and tuning curves. Diagram of surface EMG electrode and sample EMG tuning curves from representative subjects taken from early (dashed blue) and late (solid black) segments within trial. Vertical lines represent preferred direction from early (dashed blue) and late (solid black) segments within trial.



Supplementary Figure 3 Effect of penalty parameter in slow learning rate condition only. A. Left: Average magnitude of the decoder matrix (norm) as a function of time in the trial for low (dashed light orange) and high (solid dark orange) decoder penalty terms (N = 14, median with shaded area indicating the interquartile range). Right: Boxplots are average decoder effort across the trial for each subject (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, **$p < 0.001$). **B.** Left: Average magnitude of the user encoder matrix (norm) as a function of time in the trial for low (dashed light purple) and high (solid dark purple) decoder penalty terms (N = 14, median with shaded area indicating the interquartile range). Right: Boxplots are average effort for each subject across the trial (N = 14, median with shaded area indicating the interquartile range; Wilcoxon signed-rank test, *$p < 0.05$). **C.** Percent change in error from the start of the trial (first 30 seconds) to the end of the trial (last 30 seconds), separated by high (dark gray) and low (light gray) decoder penalty term conditions (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, ns > 0.05). **D.** Left: Average cursor speed as a function of time in the trial for low (light gray) and high (dark gray) decoder penalty terms (N = 14, median with shaded area indicating the interquartile range). Right: Boxplots are average cursor speed across the trial for each subject (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, **$p < 0.001$).



Supplementary Figure 4 Decoder initialization slightly influences decoder-encoder pairs. A. Model predictions. All panels show the gradient field of the user and decoder cost functions. Purple (user) and orange (decoder) curves show nullclines (where the agent's gradient equals 0) that intersect at stationary points (black stars). Decoder initialization D1 (light orange) and initialization D2 (dark orange) are noted on the vertical axis of the diagram. Assumed user initialization (purple) is noted on the horizontal axis. **B.** Left: Average magnitude of the decoder matrix (norm) as a function of time in the trial for D1 (solid light orange) and D2 (dashed dark orange) initializations (N = 14, median with shaded area indicating the interquartile range). Right: Boxplots are average decoder effort across the trial for each subject (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, ns > 0.05). **C.** Left: Average magnitude of the user encoder matrix (norm) as a function of time in the trial for D1 (solid dark purple) and D2 (dashed light purple) decoder initializations (N = 14, median with shaded area indicating the interquartile range). Right: Boxplots are average effort for each subject across the trial (N = 14, median with shaded area indicating the interquartile range; Wilcoxon signed-rank test, ns > 0.05). **D.** Percent change in error from the start of the trial (first 30 seconds) to the end of the trial (last 30 seconds), separated by high (dark gray) and low (light gray) decoder penalty term conditions (N=14, median with shading indicates interquartile range; Wilcoxon signed-rank test, ns > 0.05). **E.** Last minute in trial of product of the average decoder matrix of each initialization with first-order feedforward (F_1) contributions of the average encoder matrix of each initialization separated by learning rate. Fast learning rate conditions are shaded gray. The matched conditions are the decoders and encoders of the same initialization and the mismatched conditions are the decoders and encoders of different initializations (N=28, median with shading indicates interquartile range; Wilcoxon signed-rank test, ns > 0.05; *p < 0.05; **p < 0.001). **F.** Last minute in trial of product of the average decoder matrix of each initialization with first-order feedback (B_1) contributions of the average encoder matrix of each initialization, separated by learning rate. Fast learning rate conditions are shaded gray. The matched conditions are the decoders and encoders of the same initialization and the mismatched conditions are the decoders and encoders of different initializations (N=28, median with shading indicates interquartile range; Wilcoxon signed-rank test, ns > 0.05; *p < 0.05; **p < 0.001).