1   **Extrinsic and Intrinsic Dynamics in Movement Intermittency**

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7   **Abstract**

8   What determines how we move in the world? Motor neuroscience often focusses either on intrinsic
9   rhythmical properties of motor circuits or extrinsic sensorimotor feedback loops. Here we show that
10   the interplay of both intrinsic and extrinsic dynamics is required to explain the intermittency observed
11   in continuous tracking movements. Using spatiotemporal perturbations in humans, we demonstrate
12   that apparently discrete submovements made 2-3 times per second reflect constructive interference
13   between motor errors and continuous feedback corrections that are filtered by intrinsic circuitry in
14   the motor system. Local field potentials in monkey motor cortex revealed characteristic signatures of
15   a Kalman filter giving rise to both low-frequency cortical cycles during movement, and delta
16   oscillations during sleep. We interpret these results within the framework of optimal feedback control,
17   and suggest that the intrinsic rhythmicity of motor cortical networks reflects an internal model of
18   external dynamics which is used for state estimation during feedback-guided movement.

19   **Keywords**

20   Submovements, movement intermittency, motor cortex, optimal feedback control

21   **Introduction**

22   Many visually-guided movements are characterized by intermittent speed fluctuations. For example
23   while tracking slowly-moving targets, humans make around 2-3 submovements per second. Although
24   first described over a century ago (Woodworth, 1899; Craik, 1947; Vince, 1948) the cause of
25   movement intermittency remains debated. Submovements often disappear in the absence of vision
26   (Miall *et al.*, 1993a) and are influenced by feedback delays (Miall, 1996), suggesting their timing
27   depends on extrinsic properties of visuomotor feedback loops. However, rhythmicity is also reported
28   in the absence of feedback (Doeringer and Hogan, 1998), and it has been suggested that an internal
29   refractory period, clock or oscillator parses complex movements into discrete isochronal segments
30   (Viviani and Flash, 1995; Russell and Sternad, 2001; Loram *et al.*, 2006; Hogan and Sternad, 2012).
31   Cyclical dynamics within motor cortical networks with a time period of 300-500ms may reflect the
32   neural correlates of such an intrinsic oscillator (Churchland *et al.*, 2012; Hall *et al.*, 2014). During
33   continuous tracking, each submovement is phase-locked to a single cortical cycle, giving rise to low-
34   frequency coherence between cortical oscillations and movement speed (Jerbi *et al.*, 2007; Hall *et al.*,
35   2014; Pereira *et al.*, 2017). Moreover, this rhythmicity appears conserved across a wide range of
36   behaviors and even shares a common dynamical structure with delta oscillations during sleep (Hall *et*
37   *al.*, 2014). It has been proposed that recurrent networks express these intrinsic dynamics as an 'engine
38   of movement' responsible for internal generation and timing of the descending motor command
39   (Churchland *et al.*, 2012). Nevertheless, the interplay between intrinsic rhythmicity and extrinsic
40   feedback remains poorly understood. For example, if feedback delays influence submovement timing
41   they might be expected also to alter the frequency of cortical cycles. However, this seems
42   incompatible with conserved intrinsic dynamics evident across multiple behavioral contexts including
43   sleep. Moreover, the precise computational role of such intrinsic circuitry remains uncertain.

44 In recent years, stochastic optimal control theory has emerged as an influential computational
45 approach to understanding human movement, due to recognition of the impact of noise in both motor
46 and sensory signals on behavior (Todorov and Jordan, 2002; Scott, 2004). In the presence of delayed,
47 uncertain measurements, feedback should act on optimal estimates of the discrepancy between
48 desired goals and current motor states. Optimal feedback control (OFC) explains many features of
49 movement but it is unclear whether optimality principles alone can account for movement
50 intermittency. Various modifications to OFC have been proposed, for example explicitly including a
51 refractory period between submovements (Gawthrop *et al.*, 2011), but theoretical justification for
52 these additions is lacking. Here we present evidence from visuomotor tracking by humans and non-
53 human primates in support of an OFC-based model of movement intermittency that does not require
54 explicit parsing of submovements. Instead, continuous integration of external feedback with internal
55 state estimation provides a framework for understanding both extrinsic and intrinsic contributions to
56 intermittency. This can account for many puzzling features of submovements, and provides a
57 parsimonious explanation for conserved cyclical dynamics in motor cortex networks during behavior
58 and sleep.

59

60 **Results**

61 *Submovements reflect constructive interference between motor noise and delayed feedback*
62 *corrections*

63 Human subjects generated bimanual isometric index finger forces to track targets that moved in 2D
64 circular trajectories with constant speed (Fig. 1A). We measured intermittency in the angular velocity
65 of the cursor (Fig. 1B, C), using spectral analysis to quantify submovement frequencies. Under normal
66 feedback conditions, power spectra generally exhibited a principal peak at around 2 Hz (Fig. 1D) and
67 this frequency was only slightly affected by target speed (Figure S1), consistent with previous
68 descriptions of movement intermittency (Miall, 1996). However, submovement frequencies were
69 markedly altered when visual feedback of the cursor was delayed relative to finger forces. With delays
70 of 100 and 200 ms, the frequency of the primary peak reduced to around 1.4 and 1 Hz respectively
71 (Fig. 1D, Fig. S1, Fig. S2), suggesting submovement timing was not determined by a fixed internal clock
72 but depended instead on extrinsic feedback properties. Interestingly, a further peak appeared at
73 approximately three times the frequency of the primary peak and, with increased delays of 300 and
74 400 ms, a 5th harmonic was observed. The time-periods of the first, third and fifth harmonics were
75 linearly related to extrinsic delay times with gradients of 1.89 ± 0.20, 0.59 ± 0.04 and 0.33 ± 0.11
76 respectively (Fig. 1E, Table S1).

77 These results are consistent with a feedback controller responding to broad-spectrum (stochastic)
78 tracking errors introduced by noise in the motor output, for which the response is delayed by time τ
79 (Fig. 1F). In signal processing terms, subtracting a delayed version from the original signal is known as
80 comb filtering. For motor noise components with a time period, $T = {}^{\tau}/_1, {}^{\tau}/_2, {}^{\tau}/_3 \dots$, delayed
81 feedback accurately reflects current errors, resulting in regularly spaced notches in the amplitude
82 response of the system (Fig. 1G) and attenuation from the resultant cursor movement through
83 destructive interference. By contrast, for motor noise with a time-period, $T = {}^{2\tau}/_1, {}^{2\tau}/_3, {}^{2\tau}/_5 \dots$,
84 delayed feedback is exactly out-of-phase with the current error. Thus, corrective movements
85 exacerbate these components through constructive interference leading to spectral peaks at
86 frequencies:

87 $$f = {}^1/_T = {}^N/_{2(\tau_{\text{int}} + \tau_{\text{ext}})} \text{ with } N = 1, 3, 5 \dots \qquad\qquad \text{(Equ. 1)}$$

2

88 Submovement frequencies in our data approximately matched this model assuming the total feedback
89 delay comprised the experimental manipulation τ_{ext} added to a constant physiological response
90 latency τ_{int} of around 300 ms (Table S1), comparable to visual reaction times.

91 Note that in this interpretation, intermittency arises not from active generation of discrete
92 submovement events but as a byproduct of continuous, linear feedback control with inherent time
93 delays. Submovement frequencies need not be present in the smooth target movement, nor do they
94 arise from controller non-linearities. Instead these frequencies reflect components of broad-band
95 motor noise that are exacerbated by delayed feedback corrections. To seek further evidence that
96 intermittency arises from constructive interference between motor noise and delayed feedback
97 corrections, we generated artificial errors during target tracking by adding spatial perturbations to the
98 cursor displayed to subjects. Within individual trials, a sinusoidal displacement was applied in a
99 direction aligned to target motion and at a frequency between 1-5 Hz. Perturbation amplitudes were
100 scaled to have equivalent peak angular velocities (equal to the angular velocity of the target). Our
101 hypothesis was that artificial errors at submovement frequencies would be harder to track (because
102 of constructive interference) than perturbations at frequencies absent from the velocity spectrum.

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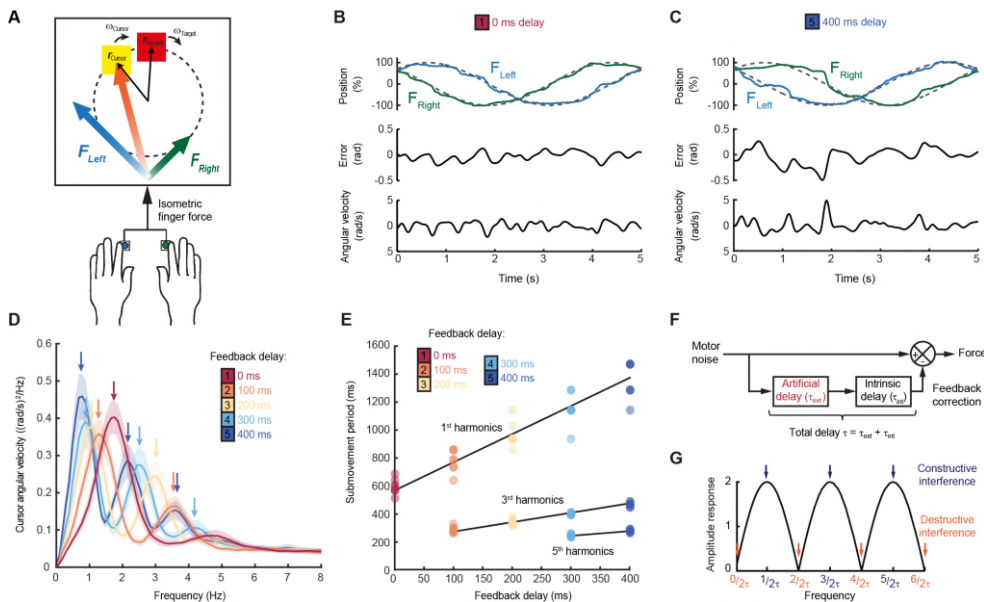
Figure 1. Movement intermittency during visuomotor tracking depends on feedback delays. (A) Schematic of human tracking task. Bimanual isometric finger forces control 2D cursor position to track slow, circular target motion. Kinematic analyses use the angular velocity of the cursor subtended at the screen center screen. (B) Example force (*top*), angular error (*middle*) and cursor angular velocity (*bottom*) traces during target tracking with no feedback delay. Submovements are evident as intermittent fluctuations in angular velocity. (C) Example movement traces with 400 ms feedback delay. (D) Power spectra of cursor angular velocity with different feedback delays between 0–400 ms. Average of 8 subjects, shading indicates standard error of mean (s.e.m.). See also Figure S2. (E) Submovement periods (reciprocal of the peak frequency for each harmonic) for all subjects with different feedback delays. See also Table S1. (F) Schematic of a simple delayed feedback controller. (G) Amplitude response of the system shown in (F), known as a comb filter.

Figure 1—source data 1. This spreadsheet contains the frequencies of spectral peaks and associated regression analysis shown in Figure 1D,E. These data can be opened with Microsoft Excel or with open-source alternatives such as OpenOffice.

119   Figure 2A shows example tracking behavior with a 2 Hz perturbation. Note that the peak angular
120   velocity of force responses (*black line*, calculated from the subject's finger forces) occurred around
121   the same time as the peak angular velocity of the perturbation (*green line*). As a result, the angular
122   velocity of the cursor (*yellow line*, reflecting the combination of the subject's forces with the
123   perturbation) exhibited pronounced oscillations that were larger than the perturbation. Figure 2B
124   shows performance in the same task when visual feedback was delayed by 200 ms. In this condition,
125   peaks in force velocity coincided with perturbation troughs, attenuating the disturbance to cursor
126   velocity. Figure 2C,D and Figure S3 overlay cursor velocity spectra in the presence of each perturbation
127   frequency (with feedback delays of 0 and 200 ms). As previously, in the absence of feedback delay the
128   frequency of submovements was around 2 Hz. Correspondingly, perturbations at 2 Hz induced a large
129   peak in the cursor velocity spectrum, indicating that the artificial error was not effectively tracked. By
130   contrast, with a feedback delay of 200 ms the cursor velocity spectrum with a 2 Hz perturbation was
131   attenuated. The largest spectral peaks were instead associated with 1 and 3 Hz perturbations,
132   matching the frequencies of submovements in this delay condition. Figure 2E shows the amplitude
133   response of cursor movements (the relative amplitude of cursor movements phase-locked to the
134   perturbation) at each frequency for both delay conditions. Cursor amplitude responses greater than
135   unity at 2 Hz (with no delay), and at 1 and 3 Hz (with 200 ms delay) indicate exacerbation of
136   intermittencies introduced by artificial errors at submovement frequencies. Analysis of variance
137   (ANOVA) with two factors (delay time and perturbation frequency) revealed a highly significant
138   interaction (n=8 subjects, $F_{4,70}$=110.2, P<0.0001), confirming the interdependence of feedback delays
139   and frequencies of constructive/destructive interference.

140   *Feedback responses reflect filtered visual discrepancies*

141   It is clear from the velocity spectra in Figure 1D that not all submovement harmonics predicted by the
142   comb filter model were present with the same amplitude within our tracking data. Rather,
143   intermittency peaks for each delay condition were embedded within a broad low-pass envelope. Next
144   we considered the origin of this delay-independent envelope. Our first hypothesis was that this might
145   reflect the spectral content of motor noise during tracking. However we could reject this as the sole
146   contributing factor by examining the force amplitude response to perturbations (the relative
147   amplitude of force responses phase-locked to the perturbation). Figures 2F,G and Figure S4 show
148   power spectra of the angular velocity derived from subject's forces, under feedback delays of 0 and
149   200 ms. Figure 2H shows the corresponding force amplitude response at each frequency. Analyzed in
150   this way, amplitude responses were largely independent of extrinsic delay. However, as with
151   submovement peaks, feedback responses were also attenuated at higher frequencies. A two-factor
152   ANOVA confirmed a significant main effect of frequency (n=8 subjects, $F_{4,70}$=36.3, P<0.0001) but not
153   delay time ($F_{1,70}$=3.1, P=0.08), and only a weakly significant interaction ($F_{4,70}$=2.9, P=0.03). Moreover,
154   the phase delay of force responses was reduced at low frequencies (Fig. 2I). As with the amplitude
155   response, there was a significant effect of frequency ($F_{4,70}$=9.5, P<0.0001) but not extrinsic delay ($F_{1,70}$
156   =2.6, P=0.12) on this phase delay, and no significant interaction ($F_{4,70}$=0.7, P=0.6). In other words,
157   feedback corrections to artificial noise with equal amplitude at different frequencies revealed
158   characteristic signatures of a filter that was independent of extrinsic feedback delays. Moreover, this
159   intrinsic filter had the appropriate bandwidth to account for attenuation of intermittency at higher
160   frequencies.

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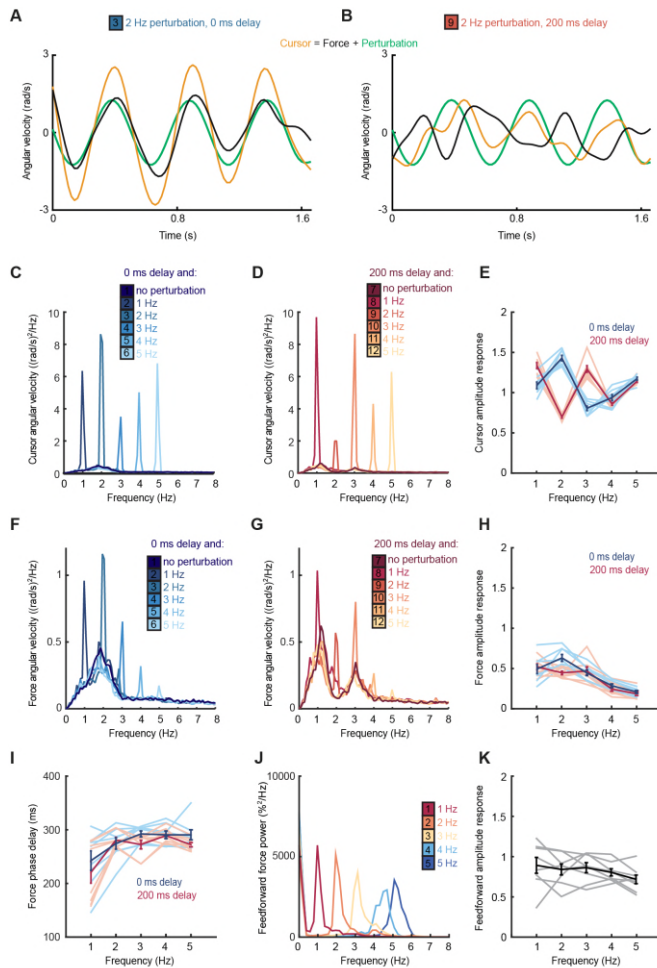
Figure 2. Frequency responses and phase delays to artificial motor errors. (A) Example force (*black*) and cursor (*yellow*) angular velocity traces in the presence of a 2 Hz perturbation (*green*). No feedback delay is added. The force response and perturbation sum to produce large fluctuations in cursor velocity. (B) Comparable data with a feedback delay of 200 ms. In this condition, force responses cancel the perturbation leading to an attenuation of intermittency. (C) Power spectra of cursor angular velocity with 1–5 Hz perturbations and no feedback delay. Average of 8 subjects. See also Figure S3. (D) Power spectra of cursor angular velocity with 1–5 Hz perturbations and 200 ms feedback delay. (E) Cursor amplitude response to 1–5 Hz perturbations with no feedback delay (*blue*) and 200 ms feedback delay (*red*) for individual subjects. Also shown is average ± s.e.m. of 8 subjects. (F) Power spectra of force angular velocity with 1–5 Hz perturbations and no feedback delay. See also Figure S4. (G) Power spectra of force angular velocity with 1–5 Hz perturbations and 200 ms feedback delay. (H) Force amplitude response to 1–5 Hz perturbations with no feedback delay (*blue*) and 200 ms feedback delay (*red*). Also shown is average ± s.e.m. of 8 subjects. (I) Intrinsic phase delay of force response to 1–5 Hz perturbations with no feedback delay (*blue*) and 200 ms feedback delay (*red*). Also shown is average ± s.e.m. of 8 subjects. (J) Power spectrum of finger forces generated in the feedforward task with auditory cues at 1-5 Hz. Average of 8 subjects. See also Figure S5. (K) Force amplitude response to auditory cues in the feedforward task. Also shown is average ± s.e.m. of 8 subjects.

Figure 2—source data 2. This spreadsheet contains the cursor/force/feedforward amplitude response and phase delay data shown in Figure 2E,H,I,K. These data can be opened with Microsoft Excel or with open-source alternatives such as OpenOffice.

183 Next we considered whether this attenuation was a property of motor pathways, for example
184 reflecting filtering by the musculoskeletal system. However, it is well-known that the frequencies of
185 feedforward movements can readily exceed submovement frequencies observed during feedback-
186 guided behavior (Kunesch *et al.*, 1989). We confirmed this by asking subjects to produce force
187 fluctuations of a defined amplitude, but without providing a moving target to track. Instead we used
188 auditory cues (a metronome) to indicate the required movement frequency. In this case, subjects
189 could generate force fluctuations up to 5 Hz with little attenuation (Fig. 2J,K and Fig. S5). Therefore
190 we concluded that filtering during visuomotor tracking was not inherent to the motor pathway and
191 considered instead whether it could be a property of the feedback loop.

192

193 *Filtered feedback corrections are consistent with optimal state estimation*

194 The visual system can perceive relatively high frequencies (up to flicker-fusion frequencies above 10
195 Hz). However, for movements in the physical world, it is unlikely that high-frequency tracking
196 discrepancies reflect genuine motor errors, since this would imply implausibly large accelerations of
197 the body. Given inherent uncertainties in sensation, an optimal state estimator should attribute such
198 errors to sensory noise (as this is unconstrained by Newtonian dynamics). Formally, the task of
199 distinguishing the true state of the world from uncertain, delayed measurements can be achieved by
200 a Kalman filter which continuously integrates new evidence with updated estimates of the current
201 state evolving according to a model of the external dynamics (Fig. 3A). For simplicity we assumed the
202 1D position of the body (cursor) should move with constant velocity relative to the slow, predictable
203 target unless acted upon by accelerative forces, leading to a two-dimensional state transition model:

204
$$\begin{bmatrix} x_k \\ v_k \end{bmatrix} = \begin{bmatrix} 1 & \Delta t \\ 0 & 1 \end{bmatrix} \begin{bmatrix} x_{k-1} \\ v_{k-1} \end{bmatrix} + \begin{bmatrix} 0 \\ \Delta t \end{bmatrix} a_k \qquad \text{(Equ. 2)}$$

205 where x_k and v_k are the relative position and velocity of the cursor at time-step k, Δt is the interval
206 between time-steps, and the process noise $a_k \sim N(0, \sigma_a^2)$. Visual feedback, y_k, was assumed to
207 comprise a noisy measurement of relative position:

208
$$y_k = x_k + \varepsilon_k \qquad \text{(Equ. 3)}$$

209 with measurement noise $\varepsilon_k \sim N(0, \sigma_\varepsilon^2)$. Optimal estimates of relative position and velocity, $\hat{x}_k$ and $\hat{v}_k$
210 are given by a steady-state Kalman filter of the form:

211
$$\begin{bmatrix} \hat{x}_k \\ \hat{v}_k \end{bmatrix} = \begin{bmatrix} 1 - K_{\text{pos}} & \Delta t \\ -K_{\text{vel}} & 1 \end{bmatrix} \begin{bmatrix} \hat{x}_{k-1} \\ \hat{v}_{k-1} \end{bmatrix} + \begin{bmatrix} K_{\text{pos}} \\ K_{\text{vel}} \end{bmatrix} y_{k-1} \qquad \text{(Equ. 4)}$$

212 The innovation gains K_{pos} and K_{vel} depend only on the ratio of process to measurement noise, $\rho = $
213 $\sigma_a/\sigma_\varepsilon$, which in turn determines the cut-off frequency above which measurements are filtered
214 ($2\pi f \sim \sqrt{\rho}$). Figure 3B,C shows the amplitude response for position and velocity estimates. Note that
215 these are out of phase with each other, and therefore broadband input results in a complex cross-
216 spectral density between them. The imaginary component of this cross-spectrum exhibits a
217 characteristic resonance peak (Fig. 3D). Feedback delays can be accommodated by projecting the state
218 estimate forward in time:

219
$$\hat{z}_k = \begin{bmatrix} 1 & \tau_{\text{int}} \end{bmatrix} \begin{bmatrix} \hat{x}_k \\ \hat{v}_k \end{bmatrix} \qquad \text{(Equ. 5)}$$

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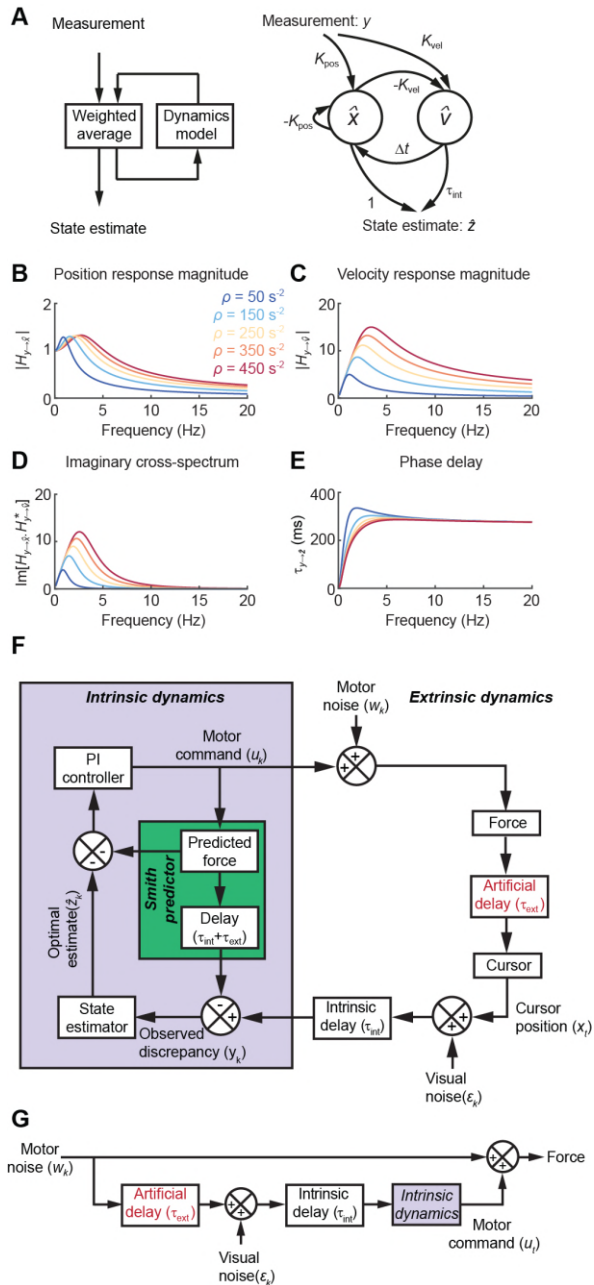
Figure 3. State estimation with a Kalman filter. (A) *Left:* Schematic of a Kalman filter. Noisy measurements are combined with an internal model of the external dynamics to update an optimal estimate of current state. *Right:* A dynamical system for optimal estimation of position, based on an internal model of position and velocity. (B, C) Magnitude response of transfer function from measurement to position and velocity estimates for the Kalman filter with different ratios of process to measurement noise (ρ). (D) Imaginary component of cross-spectrum between position and velocity transfer functions. (E) Phase delay of optimal estimate of position based on delayed measurement of position. (F) Schematic of optimal feedback controller model incorporating state estimation and a Smith Predictor architecture to accommodate feedback delays. (G) Simplified rearrangement of (F), showing the feedforward relationship between motor noise and force output. This rearrangement is possible because the Smith Predictor prevents motor corrections reverberating multiple times around the feedback loop.

7

235   The phase delay of the optimal position estimate for the current state, $\hat{z}_k$, falls towards zero at low
236   frequencies, consistent with successful prediction on the basis of delayed measurement (Fig. 3E). This
237   steady-state Kalman filter was incorporated within a 1D feedback controller (Fig. 3F; see Methods for
238   details) which also included an internal feedback loop to cancel the sensory consequences of motor
239   commands. This architecture, known as a Smith Predictor (Miall *et al.*, 1993b; Abe and Yamanaka,
240   2003), prevents corrections from reverberating around the external feedback loop, such that the
241   resultant closed-loop behavior is formally equivalent to the simpler feedforward system shown in
242   Figure 3G. This rearrangement provides a useful intuition about our behavioral results. Tracking errors
243   (due to motor noise) drive feedback corrections that are delayed, corrupted (by sensory noise) and
244   filtered (by intrinsic dynamics). The power spectrum of the resultant movement reflects
245   constructive/destructive interference between feedback corrections and the original tracking error.

246   This simple model readily accounted for the main features of our human data, including the cursor
247   amplitude response to perturbations (Fig. 4A-E), and the low-pass filtering (Fig. 4F-H) and phase delay
248   (Fig. 4I) of force responses. Moreover, because of frequency-dependent phase delays introduced by
249   state estimation, the model predicted that precise frequencies of submovement peaks should deviate
250   slightly from those calculated using a constant physiological response latency. This effect was
251   confirmed in our behavioral data by calculating (with Equ. 1) the intrinsic delay time corresponding to
252   each spectral harmonic under all feedback delays (Fig. 1D). This intrinsic delay time was positively
253   correlated with the frequency of the harmonic (n=11 spectral peaks, R=0.85, P=0.0009; Fig. 4J). Finally,
254   overall tracking performance (as measured by the root mean squared positional error over time)
255   matched well with subjects' actual performance across conditions (Fig. 4K). Note that irrespective of
256   delay, the lowest frequency perturbation was associated with the greatest positional error (since
257   perturbations had equal peak-to-peak velocity and were therefore larger in amplitude at low
258   frequencies). However, performance was most affected by the 1 Hz perturbation with a 200 ms delay,
259   corresponding to a frequency of constructive interference.

260   In summary, amplitude and phase responses to perturbations during human visuomotor tracking
261   provide compelling evidence for intrinsic filtering of measurement noise from feedback corrections,
262   while a plausible computational justification is provided by optimal state estimation. Moreover, while
263   this interpretation is derived from computational principles, the schematic on the right of Fig. 3A
264   suggests how a steady-state Kalman filter could be implemented by neural circuitry. Two neural
265   populations representing position and velocity should evolve according to Equ. 4 and thus exhibit a
266   resonance peak in their imaginary cross-spectrum. To seek further evidence for the neural
267   implementation of such a filter we turned to intracortical recordings in non-human primates.

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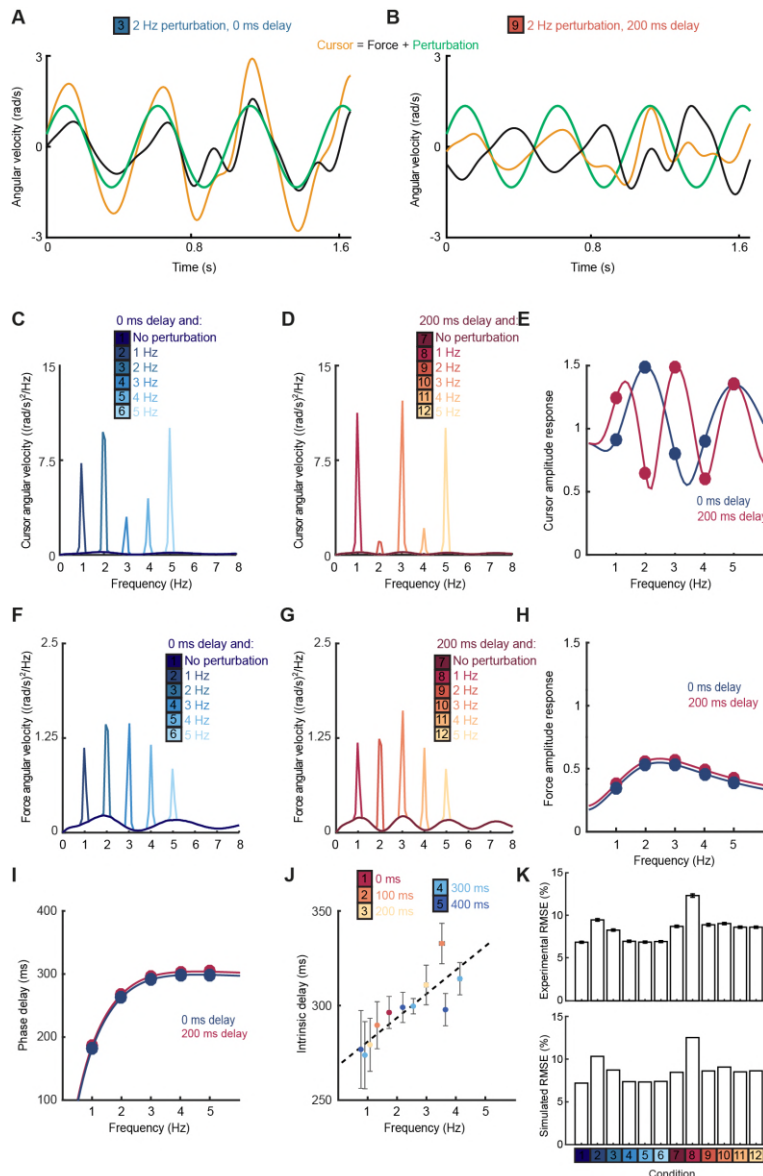
Figure 4. OFC model reproduces human behavioral data. (A) Simulated tracking performance of the OFC model with a 2 Hz sinusoidal perturbation and no feedback delay. (B) Simulated tracking performance of the OFC model with a 2 Hz sinusoidal perturbation and 200 ms feedback delay. (C) Power spectrum of simulated cursor velocity with 1–5 Hz perturbations and no feedback delay. (D) Power spectrum of simulated cursor velocity with 1–5 Hz perturbations and 200 ms feedback delay. (E) Simulated cursor amplitude response to 1–5 Hz perturbations with no feedback delay (*blue*) and 200 ms feedback delay (*red*). (F) Power spectrum of simulated force velocity with 1–5 Hz perturbations and no feedback delay. (G) Power spectrum of simulated force velocity with 1-5 Hz perturbations and 200 ms feedback delay. (H) Simulated force amplitude response to 1–5 Hz perturbations with no feedback delay (*blue*) and 200 ms feedback delay (*red*). (I) Simulated intrinsic phase delay of force responses to 1–5 Hz perturbations with no feedback delay (*blue*) and 200 ms feedback delay (*red*). (J) Intrinsic delay times corresponding to all submovement peaks/harmonics in Figure 1D, plotted against the frequency of the peak. Error bars indicate s.e.m. across 8 subjects. (K) *Top:* Positional inaccuracy of human tracking for all conditions quantified as root mean squared error (RMSE). Average ± s.e.m. of 8 subjects. *Bottom:* RMSE of simulated tracking for all conditions.

285

286   *Movement intermittency in a non-human primate tracking task*

287   We were interested in whether cyclical motor cortex dynamics could reflect the neural correlates of
288   the two interacting neural populations described above, and thereby account for filtering of feedback
289   responses during visuomotor tracking. We therefore analyzed local field potential (LFP) recordings
290   from monkey primary motor cortex (M1) during a center-out isometric wrist torque task that we have
291   used previously to characterize both submovement kinematics and population dynamics (Hall *et al.*,
292   2014). Figure 5 shows example tracking behavior (Fig. 5A), radial cursor velocity (Fig. 5B) and
293   multichannel LFPs (Fig. 5C) as monkeys moved to peripheral targets under two feedback delay
294   conditions. Movement intermittency was apparent as regular submovement peaks in the radial cursor
295   velocity. Moreover LFPs exhibited low-frequency oscillations during movement, with a variety of
296   phase-shifts present on different channels. Principal component analysis (PCA) yielded two orthogonal
297   components of the cortical cycle (Fig. 5E), and the close coupling with submovements was revealed
298   by overlaying the cursor velocity profile onto, in this case, the second principal component (PC) (Fig.
299   5E).

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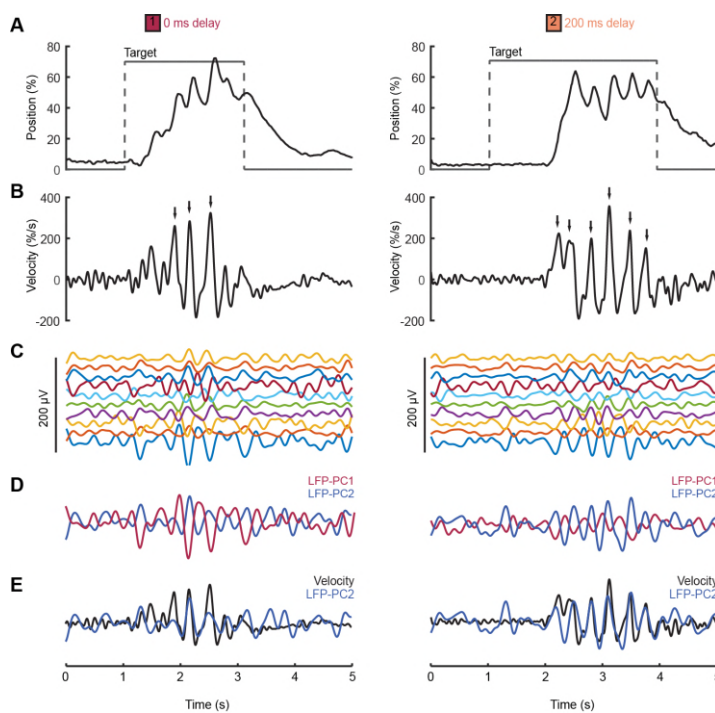
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302   **Figure 5. Movement intermittency in a non-human primate tracking task.** (A) Radial cursor position
303   during a typical trial of the center-out isometric wrist torque task under two different feedback delay
304   conditions. Data from Monkey U. (B) Radial cursor velocity. Arrowheads indicate time of
305   submovements identified as positive peaks in radial cursor velocity >150%/s. (C) Low-pass filtered,
306   mean-subtracted LFPs from M1. (D) First two principal components (PCs) of the LFP. (E) The second
307   LFP-PC overlaid on the radial cursor velocity.

308

309   As with humans, in the absence of feedback delay the cursor velocity (after removing task-locked
310   components, see Methods) was dominated by a single spectral peak around 2-3 Hz (Fig. 6A,E; *top*
311   *red traces*). A broad peak at approximately the same frequency was also observed in average LFP
312   power spectra (Fig. 6B,F), while coherence analysis confirmed consistent phase-coupling between

10

313 LFPs and cursor velocity (Fig. 6C,G). We also calculated imaginary coherence spectra between pairs
314 of LFPs (see Methods) to separate local signal components with a consistent, non-zero phase
315 difference from in-phase components (e.g. due to volume conduction from distant sources), which
316 revealed more clearly the 2-3 Hz LFP oscillation (Fig. 6D,H). An obvious interpretation of these
317 results could be that oscillatory activity in the motor system drives submovements in a feedforward
318 manner. In this case we would expect the frequency of the cortical oscillation to reliably reflect the
319 intermittency observed in behavior.

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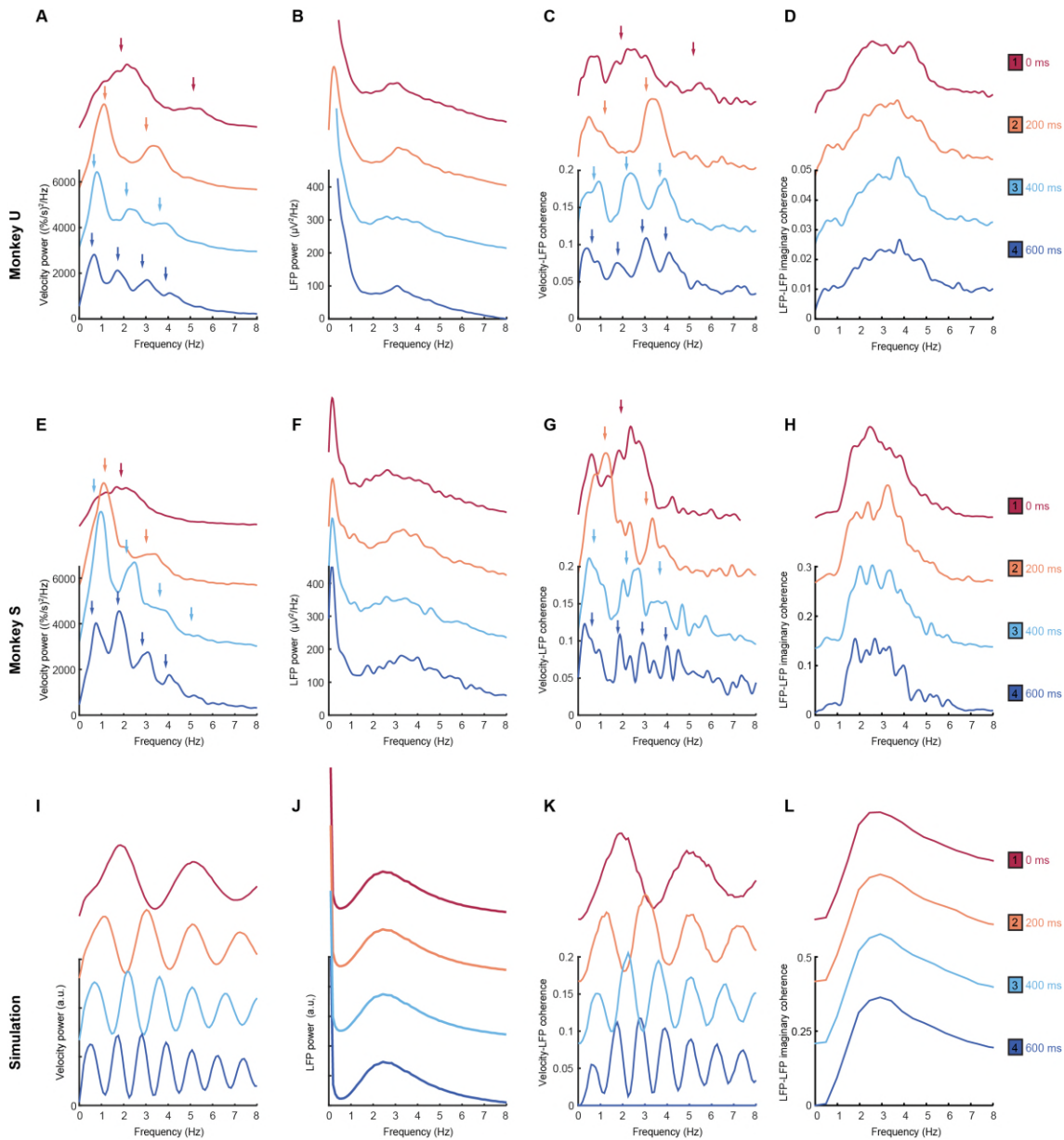
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322 **Figure 6. Frequency-domain analysis reveals delay-dependent and delay-independent spectral**
323 **features.** (A) Power spectrum of radial cursor speed with 0–600 ms feedback delay. Traces have been
324 off-set for clarity. Arrows indicate expected frequencies of peaks from OFC model. Data from Monkey
325 U. (B) Average power spectrum of M1 LFPs. (C) Average coherence spectrum between radial cursor
326 speed and all M1 LFPs. (D) Average imaginary coherence spectrum between all pairs of M1 LFPs. (E-
327 H) As above, but for Monkey S. (I-L) Simulated power and coherence spectra produced by the OFC
328 model.

11

329   *Feedback delays dissociate intrinsic and extrinsic contributions to intermittency*

330   With increasing feedback delays, submovement peaks in monkeys (Fig. 6A,E) exhibited a pattern
331   similar to that seen with human subjects. The fundamental frequency was reduced, while odd
332   harmonics grew more pronounced as they came below about 4 Hz. Moreover, coherence spectra
333   between cursor velocity and LFP (Fig. 6C,G) revealed peaks at both fundamental and harmonic
334   frequencies. Surprisingly however, the power spectrum of the LFP (Fig. 6B,F) was unaffected by
335   feedback delay, with a single broad peak in the delta band persisting throughout. Moreover, imaginary
336   coherence spectra between pairs of LFPs were also unchanged (Fig. 6D,H). These results appear
337   incompatible with the hypothesis that motor cortical oscillations drive movement intermittency, and
338   instead demonstrate a dissociation between delay-dependent submovements and the conserved
339   rhythmicity of LFPs.

340   We next identified submovements from peaks in the radial cursor speed, in order to examine the
341   temporal profile of their associated LFPs. Submovement-triggered averages (SmTAs) of LFPs exhibited
342   multiphasic potentials around the time of movement, as well as a second feature following
343   submovements with a latency that depended on extrinsic delay (Fig. 7A, Fig. S6A). This feature was
344   revealed more clearly by reducing the dimensionality of the LFPs with PCA (Fig. 7B, Fig. S6B). Note that
345   if submovements reflect interference between stochastic motor errors and feedback corrections, a
346   submovement in the positive direction can arise from two underlying causes. First, it may be a positive
347   correction to a preceding negative error. In this case, cortical activity associated with the feedback
348   correction should occur around time zero. Second, the submovement may itself be a positive error
349   which is followed by a negative correction, and the associated cortical activity will hence be delayed
350   by the feedback latency. Since the SmTA pools submovements arising from both causes, this accounts
351   for two features with opposite polarity separated by the feedback delay. Note also that SmTAs of
352   cursor velocity similarly overlay (negative) tracking errors preceding (positive) feedback corrections,
353   and (negative) feedback corrections following (positive) tracking errors, evident as symmetrical
354   troughs on either side of the central submovement peak (Fig. 7C, Fig. S6C).

355   Importantly however, LFP oscillations around the time of submovements appeared largely unaffected
356   by delay. To visualize this, we projected the SmTAs of multichannel LFPs onto the same PC plane. For
357   all delay conditions, LFPs traced a single cycle with the same directional of rotation and comparable
358   angular velocity (Fig. 7D, Fig. S6D). The period of these cycles (approx. 300 ms) matched the frequency
359   of imaginary coherence between LFPs (approx. 3 Hz), as expected since signals with a consistent phase
360   difference will be orthogonalized by PCA and appear as cyclical trajectories in the PC plane. In other
361   words, although the precise frequency of submovements depends on extrinsic delays in visual
362   feedback, the constant frequency of associated LFP cycles reveals conserved intrinsic dynamics within
363   population activity in the motor cortex. Note also that the resonant frequency of these dynamics
364   matches the intrinsic filtering of feedback responses observed in our human experiments.

365
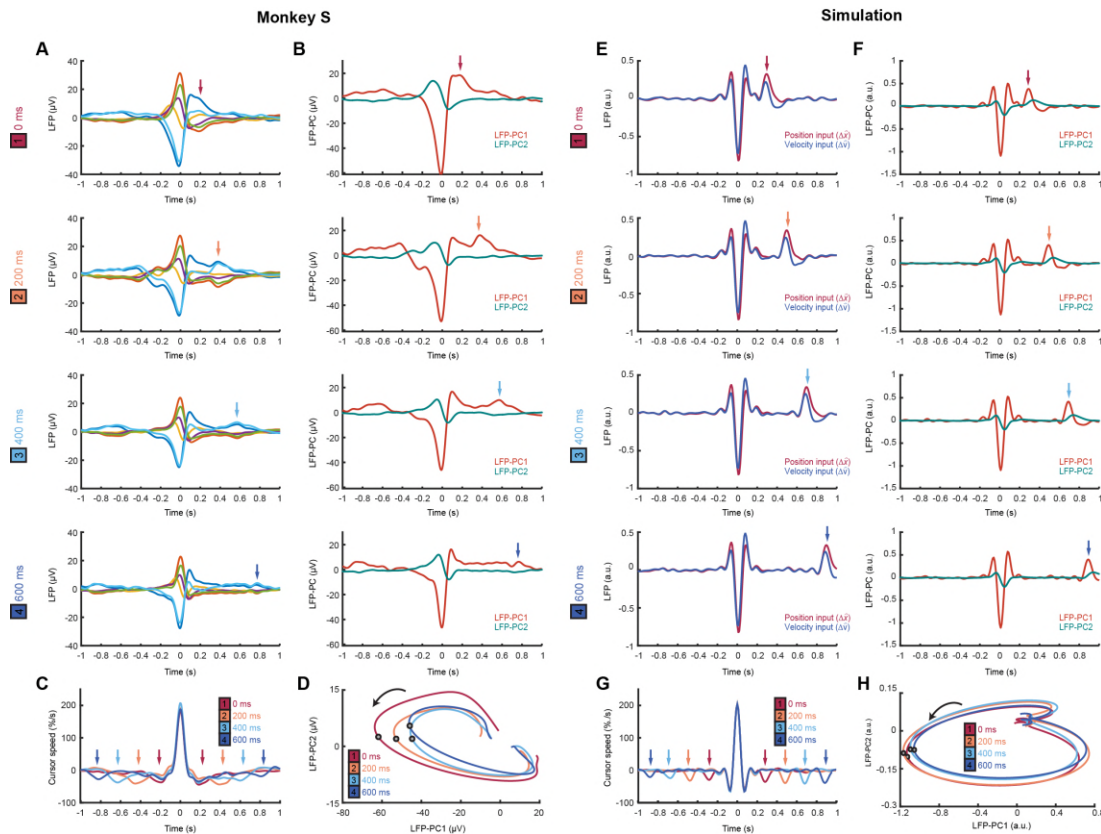
Figure 7. Submovement-triggered averages of M1 LFPs. (A) Average low-pass filtered LFPs from M1, aligned to the peak speed of submovements with 0–600 ms feedback delay. Arrows indicate second feature following submovement by an extrinsic delay-dependent latency. Data from Monkey S. See also Figure S6. (B) Average of first two LFP-PCs aligned to submovements. (C) Average low-pass filtered cursor speed, aligned to submovements. Arrows indicate symmetrical velocity troughs at extrinsic delay-dependent latencies. (D) Average submovement-triggered LFP-PC trajectories, plotted over 200 ms either side of the time of peak submovement speed (indicated by circles). (E-H) Simulated submovement-triggered averages produced by the OFC model.

Modelling submovement-related LFP cycles and delta oscillations in sleep

These various observations can be understood using the same computational model that explained our human behavioral data (Figure S7). For simplicity, we simulated two out-of-phase components within the LFP from the total synaptic input to each of the two neural population in the state estimator. We also added common low-frequency background noise to represent volume conduction from distant sources. The simulated LFPs exhibited a broad (delay-independent) spectral peak arising from the dynamics of the recurrent network (Fig. 6J). By contrast, the resultant cursor velocity comprised the summation of motor noise and (delayed) feedback corrections, and therefore contained sharper (delay-dependent) spectral peaks due to constructive/destructive interference (Fig. 6I). Note however that coherence was nonetheless observed between LFPs and cursor velocity (Fig. 6K). Time-domain SmTAs of the simulated data also reproduced features of the experimental recordings, including delay-dependent peaks/troughs reflecting extrinsic feedback delays (Fig. 7E-G). Meanwhile, the conserved intrinsic dynamics coupling simulated neural populations resulted in consistent cyclical LFP trajectories around the time of movement (Fig. 7H) and an imaginary cross-spectrum with a single delay-independent resonance (Fig. 6L).
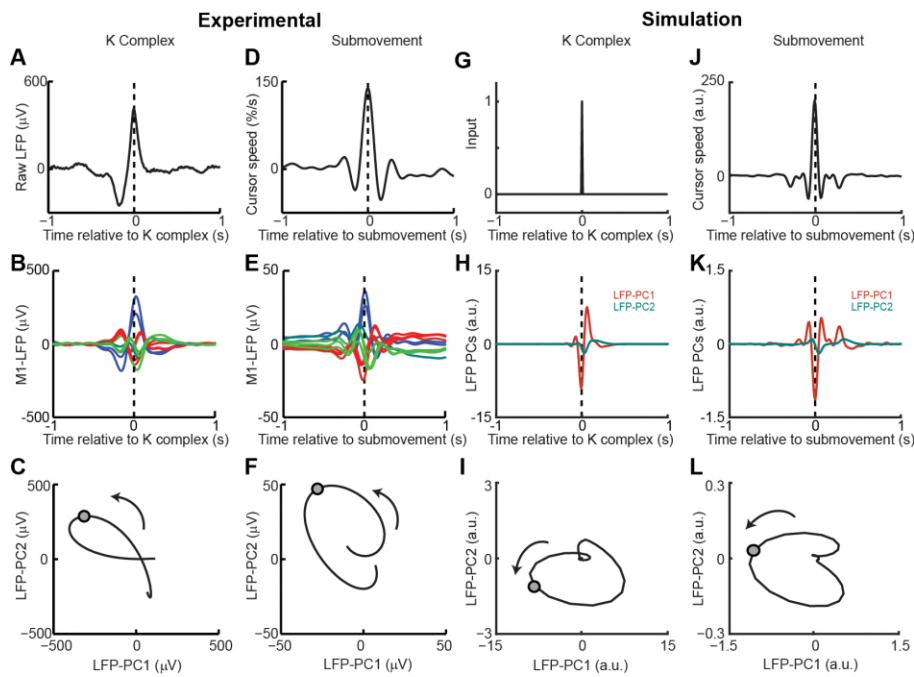
13

Figure 8. Simulated LFP dynamics during movement and sedation. (A) K-complex events in LFP from M1 recorded under ketamine sedation. (B) Average low-pass filtered multichannel LFPs aligned to K-complex events. LFPs are color-coded according to phase relative to submovements, but exhibit a similar pattern relative to K complexes. (C) Average LFP-PC trajectories aligned to K-complexes, plotted over 200 ms either side of the time of K-complex (indicated by circle), using the PC plane calculated from recordings during awake behavior. (D) Average cursor speed aligned to the peak speed of submovements. (E) Average low-pass filtered multichannel LFPs aligned to submovements. (F) Average submovement-triggered LFP-PC trajectories, plotted over 200 ms either side of the time of submovements (indicated by circle). (G) A K-complex under sedation is simulated by an impulse excitation of the OFC model, without connection to the external world. (H) Impulse response of the simulated LFP-PCs. (I) LFP-PC trajectories associated with simulated K-complexes. (J) Simulated submovement-triggered average cursor speed from the OFC model with no feedback delay. (K) Simulated submovement-triggered average LFP-PCs. (L) Simulated submovement-triggered LFP-PC trajectories. Panels A-F reproduced from Figure 4A,C,D in Hall et al. (2014) under the CC BY 3.0 license (https://creativecommons.org/licenses/by/3.0/).

Finally we examined whether the model could also account for cortical oscillations in the absence of behavior. Previously we have described a common dynamical structure within both cortical cycles during movement and low-frequency oscillations during sleep and sedation (Hall *et al.*, 2014). In particular, K-complex events under ketamine sedation (Fig. 8A), thought to reflect transitions between down- and up-states of the cortex, are associated with brief bursts of delta oscillation (Fig. 8B) (Amzica and Steriade, 1997). The relative phases of multichannel LFPs aligned to these events matches those seen during submovements (Fig. 8D,E). As a result, when projected onto the PC plane, LFPs trace similar cycles during both K-complexes (Fig. 8C) and submovements (Fig. 8F). We modelled the sedated condition by disconnecting motor and sensory connections between the feedback controller and the external world, instead providing a pulsatile input to the state estimator simulating a down-to up-state transition (Fig. 8G). Effectively, transient excitation of the state estimator elicited an impulse response reflecting its intrinsic dynamics. The simulated LFPs generated a burst of delta-

421 frequency oscillation around the K-complex (Fig. 8H) which resembled submovement-related activity
422 (Fig. 8J,K). Projecting this activity onto the same PC plane revealed consistent cycles during simulated
423 K-complexes (Fig. 8I) and submovements (Fig. 8L). Thus it appears that our computational model
424 incorporating the intrinsic dynamics of motor cortical networks could also account for the conserved
425 structure of low-frequency LFPs during movement and delta oscillations in sleep.

426

427 **Discussion**

428 *Submovement kinematics are influenced by both extrinsic and intrinsic dynamics*

429 Previous theories of intermittency have focused on either extrinsic or intrinsic explanations for the
430 regularity of submovements, but little consensus has emerged over this fundamental feature of
431 movement. There is good evidence for a common low-frequency oscillatory structure to motor cortex
432 activity across multiple behavioral states (Churchland *et al.*, 2012; Hall *et al.*, 2014; Russo *et al.*, 2018)
433 but also an influence of feedback delays on submovement timing (Miall, 1996). Experimentally
434 manipulating visual feedback with artificial time delays and spatial perturbations allowed us to
435 dissociate both contributions to submovement kinematics. We found that precise frequencies of
436 submovement peaks were determined by constructive and destructive interference between broad-
437 band motor errors and continuous, delayed feedback corrections. However, these peaks were
438 embedded within a delay-independent envelope that arose from intrinsic filtering of feedback
439 corrections. The dissociation of extrinsic and intrinsic dynamics was also evident in cortical LFPs during
440 tracking movements. Both delay-dependent feedback corrections and delay-independent cycles were
441 observed in submovement-triggered averages of LFPs. Moreover, while coherence between LFPs and
442 cursor movement exhibited delay-dependent spectral peaks, the imaginary coherence between
443 multichannel LFPs revealed a consistent dynamical structure across behaviors.

444 These apparently contradictory results could be explained by an OFC model that implemented state
445 estimation via a steady-state Kalman filter to separate process (motor) noise from measurement
446 (sensory) noise. One free parameter was tuned to achieve correspondence between simulated and
447 experimental data, namely the ratio of process to measurement noise which determined the intrinsic
448 resonance frequency around 2-3 Hz. It would be interesting in future to vary these noise
449 characteristics experimentally (e.g. by artificially degrading visual acuity or by extensively training
450 subjects) and examine the effect on perturbation responses. One possible outcome would be a change
451 to the observed resonance, although this seems to contradict the ubiquity of 2-3 Hz cortical dynamics.
452 Alternatively there may be other computational advantages to maintaining a consistent cortical
453 rhythm. For example, it is notable that 2-3 Hz intrinsic dynamics matched the frequency of the primary
454 submovement peak under unperturbed external feedback conditions, thus accentuating the
455 fundamental submovement frequency around 2 Hz while suppressing higher harmonics. This may be
456 beneficial in allowing other aspects of the visuomotor machinery to be synchronized to a single
457 rhythm, for example eye movements which are influenced by hand movement during tracking tasks
458 (Koken and Erkelens, 1992).

459

460 *Modelling isometric visuomotor tracking*

461 Several further assumptions of our modelling warrant discussion. First, to prevent control instabilities
462 associated with feedback delays we incorporated an accurate forward model of the (delayed) sensory
463 consequences of motor commands within a Smith Predictor architecture. We did not include adaptive

464 processes to calibrate the delay model, but this could be readily achieved by minimizing discrepancies
465 between an efference copy of motor commands and observed cursor movements. The accuracy of
466 tracking performance under different delay conditions (without cursor perturbations) suggests that
467 subjects could readily adapt such a forward model and this role has previously been ascribed to the
468 cerebellum (Miall *et al.*, 1993b; Streng *et al.*, 2018). By contrast, to account for the delay-independent
469 perturbation responses, we maintained the same intrinsic cortical dynamics throughout, even though
470 an optimal state estimator should similarly incorporate knowledge of feedback delays (see Equ. 5).
471 Note however that adaptation of the state estimator presents a harder computational problem, since
472 no available signals directly relate the state of the external world to delayed sensory information. Even
473 when we imposed predictable sinusoidal perturbations, we saw no evidence that subjects learnt to
474 compensate for feedback delays by altering the timing of their corrective responses within a single
475 trial. Nevertheless, it would again be interesting to examine whether state estimator dynamics might
476 adapt on a slower time-scale after extensive training with delayed feedback.

477 Finally, we were puzzled that force amplitude responses to cursor perturbations were uniformly less
478 than unity, which initially appears suboptimal for rejecting even slow perturbations. We first
479 considered that proprioceptive information (which is in conflict with vision during cursor
480 perturbations) might cause subjects to underestimate the true displacement of the cursor. However,
481 sub-unity amplitude responses were also observed in separate experiments (not shown) when
482 sinusoidal displacements were added to the target position. In this situation there was no discrepancy
483 between vision and proprioception, yet subjects consistently undershot corrections to all but the
484 lowest frequency perturbations (even in the absence of any delay). In our OFC model we instead
485 reduced amplitude responses by penalizing large changes to the motor command. This cost function
486 was minimized by proportional-integral (PI) control, which has been used in the past to model human
487 movement (Kleinman, 1974). It is more common in current optimal control models to apply cost
488 functions that penalize the absolute motor command leading to proportional feedback policies
489 (Todorov and Jordan, 2002), under the assumption that this minimizes signal-dependent noise in
490 muscles (Jones *et al.*, 2002). However, the trajectory variability observed in our isometric tracking task
491 appeared more correlated with large changes in finger forces rather than force magnitude (Figure S8),
492 providing empirical support for our choice of cost function. Derivative-dependent motor noise was
493 also evident as increased variability at high frequencies in our feedforward task (Figure S5). Since
494 submovements result from constructive interference between tracking errors and feedback
495 corrections, derivative-dependent motor noise also provides a counterintuitive but necessary
496 explanation for why the amplitude of submovements increases with target speed (Figure S1).
497 Increased intermittency cannot be a direct consequence of faster target motion, since the frequency
498 content of this motion is nevertheless low by comparison to submovements. Rather, faster tracking
499 requires a larger change in the motor command, leading to increased broad-band motor noise which,
500 after constructive interference with feedback corrections, results in more pronounced peaks at
501 submovement frequencies.

502

503 *State estimation by motor cortical population dynamics*

504 PCA of multichannel LFPs in monkey motor cortex revealed two underlying components, which we
505 interpret as arising from distinct but coupled neural populations. The cyclical movement-related
506 dynamics of these components resembled those described for M1 firing rates (Churchland *et al.*,
507 2012), which have previously been implicated in feedforward generation of movement. Specifically, it
508 was proposed that preparatory activity first develops along 'output-null' dimensions of the neural
509 state space before, at movement onset, evolving via intrinsic dynamics into orthogonal 'output-

16

510 potent' dimensions that drive muscles (Churchland *et al.*, 2010). However, this purely feedforward
511 view cannot account for our isometric tracking data, since manipulation of feedback delays dissociated
512 delay-dependent submovements from delay-independent rotational dynamics. Instead we interpret
513 these intrinsic dynamics as implementing a state estimator during continuous feedback control. We
514 used Newtonian dynamics to construct a simple two-dimensional state transition model based on
515 both the cursor-target discrepancy and its first derivative. While this undoubtedly neglects the true
516 complexity of muscle and limb biomechanics, simulations based on this plausible first approximation
517 reproduced both the amplitude response and phase delay to sinusoidal cursor perturbations in
518 humans, and the population dynamics of LFP cycles in the monkey. Note that this account also offers
519 a natural explanation of why preparatory and movement-related activity lies along distinct state-space
520 dimensions, since the static discrepancy present during preparation is encoded differently to the
521 changing discrepancy that exists during movement. At the same time, the lawful relationship between
522 discrepancy and its derivative couples these dimensions within the state estimator and is evident as
523 consistent rotational dynamics across different tasks and behavioral states.

524 It may seem unusual to ascribe the role of state estimation to M1 when this function is usually
525 attributed to parietal (Mulliken *et al.*, 2008) and premotor areas (where rotational dynamics have also
526 been reported, albeit at a lower frequency (Churchland *et al.*, 2012; Hall *et al.*, 2014). We suggest that
527 the computations involved in optimal visuomotor tracking are likely distributed across multiple
528 cortical areas including (but not limited to) M1, with local circuitry reflecting multiple dynamical
529 models of the various sensory and efference copy signals that must be integrated for accurate control.
530 Indeed, while we neglected to model the computations involved in accurately estimating our slow and
531 predictable target motion, state estimation using Kalman filters has also been suggested as a
532 mechanism by which the visual system can estimate the position of moving visual stimuli (Kwon *et al.*,
533 2015).

534 An alternative explanation for consistent rotational dynamics has recently been proposed by Russo *et*
535 *al.* (2018), based on the behavior of recurrent neural networks trained to produce different feed-
536 forward muscle patterns whilst minimizing 'tangling' between neural trajectories. It is interesting to
537 compare this with our OFC-based interpretation, since both are motivated by the problem of
538 maintaining accurate behavior in the presence of noise. Minimizing tangling leads to network
539 architectures that are robust to intrinsic noise in individual neurons, while OFC focusses on optimizing
540 movements in the face of unreliable motor commands and noisy sensory signals. Given this conceptual
541 link, it is perhaps unsurprising if recurrent neural network approaches learn implementations of
542 computational architectures such as Kalman filters that minimize the influence of noise on behavior.
543 In future it may be productive to incorporate sensory feedback into recurrent neural network models
544 of movement, as well as including intrinsic sources of neural noise in optimal control models. The
545 convergence of these frameworks may further help to reveal how computational principles are
546 implemented in the human motor system.

547

552

553 **Author contributions**

17

554   DS, KA and AJ designed the study. DS collected the human data. WX and TMH collected the monkey
555   data. DS, FG and AJ developed the computational model. DS and AJ wrote the manuscript with
556   contributions from all other authors.

557

558   **Declaration of competing interests**

559   The authors declare no competing interests.

560

561   **Materials and Methods**

562   **Human experiments**

563   <u>Subjects</u>

564   Based on pilot studies we decided in advance to use a sample size of eight subjects in each experiment.
565   In total, we recruited 11 adult subjects in total at the Institute of Neuroscience, Newcastle University.
566   Eight subjects (3 females; age 23–33; 1 left-handed) participated in both Experiment 1 (feedback
567   delay) and Experiment 2 (feedback delay and spatial perturbation). Eight subjects (3 females; age 23–
568   33; all right-handed) participated in Experiment 3 (feedforward task); 6 of these subjects also
569   participated in experiments 1 and 2. Eight subjects (3 females; age 23–33; all right-handed)
570   participated in the experiment shown in Figure S8; 7 out of these subjects also participated in
571   Experiment 3. All experiments were approved by the local ethics committee at Newcastle University
572   and performed after informed consent, which was given in accordance with the Declaration of
573   Helsinki.

574   <u>Human tracking task</u>

575   Subjects tracked a (red) target on a computer monitor by exerting bimanual isometric index finger
576   forces on two sensors (FSG15N1A; Honeywell). The target underwent uniform, slow circular motion
577   with a pseudorandom order of clockwise and anticlockwise directions across trials. Finger forces were
578   sampled at 50 samples/s (USB-6343; National Instruments) and mapped to (yellow) cursor position by
579   projecting onto two diagonal screen axis. In addition, a feedback delay (τ_{ext}) was interposed between
580   force and cursor movement. The feedback delay was kept constant through the duration of each trial
581   (lasting 20 s). We express screen coordinates in terms of the radius of target motion, $r_{\mathrm{target}} = 100\%$.
582   Tracking the target rotation thus required generating sinusoidal motion in the range of -100% to
583   +100%, corresponding to finger forces of 0 to 3.26N, with a 90° phase-shift between each hand. At the
584   end of each trial subjects were given a numerical score from 0-1000 indicating how accurately they
585   tracked the target. Subjects were instructed to attempt to maximize this score, which was calculated
586   as:

587
$$Score = \frac{1000}{T} \times \int_0^T \left(1 - e^{-\frac{\left| r_{\mathrm{cursor}}(t) - r_{\mathrm{target}}(t) \right|}{\delta}} \right) dt \qquad \text{(Equ. 6)}$$

588   where $r_{\mathrm{cursor}}(t)$ and $r_{\mathrm{target}}(t)$ are the 2D positions of the cursor and target respectively, and $\delta =$
589   50%. Apart from the experiment shown in Figure S8, all experiments used a frequency of target
590   rotation, f_{target} = 0.2 rotations per second.

591   Experiment 1 used five delay conditions (τ_{ext} = 0, 100, 200, 300, or 400 ms). Subjects performed a
592   total of 70 trials, comprising 14 of each condition presented in pseudorandom order.

593 For Experiment 2, spatial perturbations were added to the cursor position as well as time delays. The
594 perturbations were equivalent to sinusoidal modulation of the target angular velocity, but were
595 instead added to the cursor. Expressed in polar coordinates $\boldsymbol{r} = \langle r, \angle\theta \rangle$ relative to the center of the
596 screen, the target and cursor positions were thus given by:

$$\boldsymbol{r}_{\text{target}}(t) = \langle r_{\text{target}}, \angle\, \omega_{\text{target}}t \rangle \tag{Equ. 7}$$

$$\boldsymbol{r}_{\text{pert}}(t) = \langle r_{\text{target}}, \angle\, \omega_{\text{target}}t + \tfrac{\omega_{\text{target}}}{\omega_{\text{pert}}} \sin\omega_{\text{pert}}t \rangle - \boldsymbol{r}_{\text{target}}(t) \tag{Equ. 8}$$

$$\boldsymbol{r}_{\text{cursor}}(t) = \langle r_{\text{force}}(t), \angle\theta_{\text{force}}(t) \rangle + \boldsymbol{r}_{\text{pert}}(t) \tag{Equ. 9}$$

600 where $\omega_{\text{target}} = 2\pi f_{\text{target}}$ is the angular velocity of the target around the centre of the screen,
601 $\omega_{\text{pert}} = 2\pi f_{\text{pert}}$ is the angular frequency of the perturbation, and $\langle r_{\text{force}}(t), \angle\theta_{\text{force}}(t) \rangle$ is the
602 unperturbed cursor position calculated from the subject's forces at time $t - \tau_{\text{ext}}$.

603 Kinematic analyses were based on the time-varying angular velocity of the cursor subtended at the
604 center of the screen:

$$\omega_{\text{cursor}}(t) = \tfrac{d}{dt}\theta_{\text{cursor}}(t) \tag{Equ. 10}$$

606 For spatial perturbation experiments, we also calculated the angular velocity of the unperturbed
607 cursor position subtended at the center of the screen:

$$\omega_{\text{force}}(t) = \tfrac{d}{dt}\theta_{\text{force}}(t) \tag{Equ. 11}$$

609 Note that since $r_{\text{force}} \approx r_{\text{target}}$, the perturbation effectively adds a sinusoidal component to the
610 angular velocity of the cursor:

$$\omega_{\text{cursor}}(t) \approx \omega_{\text{force}}(t) + \omega_{\text{target}}\cos\omega_{\text{pert}}t \tag{Equ. 12}$$

612 Six different spatial perturbations (f_{pert} = 0, 1, 2, 3, 4, 5 Hz) combined with two feedback delays (τ_{ext}
613 = 0, 200 ms) yielded 12 conditions. Subjects performed a total of 144 trials, comprising 12 trials per
614 condition in pseudorandom order.

615 <u>Human feedforward task</u>

616 In Experiment 3, we used a unimanual isometric task in which subjects were asked to make sinusoidal
617 forces with their right index finger. Subjects received visual feedback of the cursor, but no target was
618 shown. Instead subjects were shown two amplitude boundaries to move between, and the frequency
619 of movement was cued with auditory beeps at frequencies of 1, 2, 3, 4 and 5 Hz. Subjects performed
620 a total of 15 trials, comprising three 20 s trials per frequency condition.

621

622 **Monkey experiments**

623 <u>Subjects</u>

624 We used two purpose-bred female rhesus macaques (monkey S: 6 years old, 6.6 kg; monkey U: 6 years
625 old, 8.8 kg). Animal experiments were approved by the local Animal Welfare Ethical Review Board and
626 performed under appropriate UK Home Office licenses in accordance with the Animals (Scientific
627 Procedures) Act 1986.

628 <u>Monkey tracking task</u>

629 Monkeys moved a 2D computer cursor by generating isometric flexion-extension (vertical) and radial-
630 ulnar (horizontal) torques at the wrist, measured by a 6-axis force/torque transducer (Nano25; ATI
631 Industrial Automation). Centre-out targets were presented at 8 peripheral positions in a
632 pseudorandom order. Targets were positioned at 70% of the distance to the screen edge (100%
633 corresponding to torque of 0.67 Nm). The diameter of the target and cursor ranged between 14-36%.
634 A successful trial required maintaining an overlap between cursor and peripheral target for 0.6 s after
635 which the monkeys returned to the center of the screen to receive a food reward. Visual feedback of
636 the cursor was delayed by τ_{ext} = 0, 200, 400, 600 ms throughout separate blocks of 50-70 trials each.
637 Monkey S performed the task with the right hand. Monkey U initially used the right hand and was
638 then retrained for a second period of data collection with the left hand.

639 LFP recording

640 LFPs were recorded using custom arrays of 12 moveable 50 μm diameter tungsten microwires
641 (impedance ~200 kΩ at 1 kHz) chronically implanted in contralateral wrist area of M1 under
642 sevoflurane anesthesia with postoperative analgesics and antibiotics. Head-free recordings were
643 made using unity-gain headstages followed by wide-band amplification and sampling at 24.4
644 kilosamples/s (System 3; Tucker-Davis Technologies). LFPs were digitally low-pass filtered at 200 Hz
645 and recorded at 488 samples/second.

646 Analysis of kinematics and neural data was performed on data recorded over 8 different days
647 comprising of 56 task blocks in Monkey S (no delay: 24 blocks; 200 ms delay: 13; 400 ms delay: 13; 600
648 ms delay: 6), and 89 recording days comprising of 356 task blocks in Monkey U (no delay: 89; 200 ms
649 delay: 89; 400 ms delay: 89; 600 ms delay: 89). Each task block comprised 50 (monkey S) or 70 trials
650 (monkey U).

651

652 **Analysis Methods**

653 Human data analysis

654 Spectral analysis used fast Fourier transforms (FFTs) performed on non-overlapping 512 sample-point
655 windows (approx. 10s) taken from the middle of each trial. Submovement peaks in the power spectra
656 were measured after smoothing with a seven-point moving-average.

657 For perturbation experiments, we additionally defined two complex transfer functions H_{cursor} and
658 H_{force}:

659 $$H_{\text{cursor}}\left(i\omega_{\text{pert}}\right) = \frac{2}{\omega_{\text{target}}T} \int_0^T \omega_{\text{cursor}}(t) e^{-i\omega_{\text{pert}}t} dt \qquad \text{(Equ. 13)}$$

660 $$H_{\text{force}}\left(i\omega_{\text{pert}}\right) = \frac{2}{\omega_{\text{target}}T} \int_0^T \omega_{\text{force}}(t) e^{-i\omega_{\text{pert}}t} dt \qquad \text{(Equ. 14)}$$

661 Cursor and force amplitude responses to perturbations were calculated as the magnitude of the
662 corresponding transfer functions, and the intrinsic phase delay of force responses was given by:

663 $$\tau_\varphi\left(i\omega_{\text{pert}}\right) = -\frac{\arg[H_{\text{force}}(i\omega_{\text{pert}})]}{\omega_{\text{pert}}} - \tau_{\text{ext}} \qquad \text{(Equ. 15)}$$

664 Additionally, tracking performance was quantified off-line using the root-mean-squared Euclidean
665 distance between cursor and target.

666 Monkey data analysis

667 We differentiated the magnitude of the absolute 2D torque (expressed as a percentage of the distance
668 to the edge of the screen) to obtain the radial cursor velocity. LFP channels were subjected to visual
669 inspection to reject noisy channels prior to mean-subtraction. For time-domain analysis, LFPs and
670 cursor velocities were low-pass filtered at 10 Hz. Submovements were defined as a peak radial cursor
671 speed exceeding 100%/s (monkey S) and 150%/s (monkey U). For frequency-domain analysis, we took
672 unfiltered sections of 1024 sample points from each trial (approx. 1.5 s before to 0.5 s after the end
673 of the peripheral hold period). We subtracted the trial-averaged profile from each section before
674 concatenating to yield long data sections without any consistent low-frequency components related
675 to the periodicity of the task. FFTs were calculated with overlapping Hanning windows (2^{14} sample
676 points ≈ 34 s; 75% overlap), from which we derived the following spectra:

677 Cursor power: $P_{\text{Cursor}}(f) = \frac{\sum_{m=1}^{M} F_{cursor}(f,m).F_{cursor}(f,m)^*}{M}$

678 LFP power: $P_{\text{LFP } i}(f) = \frac{\sum_{m=1}^{M} F_{\text{LFP } i}(f,m).F_{\text{LFP } i}(f,m)^*}{M}$

679 LFP-cursor coherence: $Coh_{\text{LFP } i-\text{Cursor}} = \frac{\left|\sum_{m=1}^{M} F_{\text{LFP } i}(f,m).F_{cursor}(f,m)^*\right|^2}{M.P_{\text{Cursor}}(f).P_{\text{LFP } i}(f)}$

680 LFP-LFP imaginary coherence: $Im\, Coh_{\text{LFP } i-\text{LFP } j} = \frac{\left(\text{Im}\left[\sum_{m=1}^{M} F_{\text{LFP } i}(f,m).F_{\text{LFP } j}(f,m)^*\right]\right)^2}{M.P_{\text{LFP } i}(f).P_{\text{LFP } j}(f)}$

681 where $F_{\text{LFP } i}(f,m)$ and $F_{\text{Cursor}}(f,m)$ represent Fourier coefficients at frequency f and window $m =$
682 $(1..M)$ from LFP channel i and cursor velocity respectively. All spectra were smoothed with a 16-point
683 Hanning window. In addition, LFP power and LFP-cursor coherence were averaged across all LFP
684 channels, while LFP-LFP imaginary coherence was averaged over all pairs of LFPs.

685

Modelling

687 Although both human and monkey tasks involved 2D isometric control, for simplicity we modelled
688 only a 1D controller and assumed a one-to-one mapping from control signal, u_k to position, x_k. We
689 neglected target motion and designed the controller to minimize the influence of stochastic motor
690 errors using delayed, noisy feedback of position. We set the model time step Δt = 0.01 s, intrinsic
691 feedback delay τ_{int} = 0.26 s, and the ratio of process/measurement noise ρ = 250 s^{-2} unless otherwise
692 stated. Steady-state Kalman gains were calculated using the function *kalman* in MATLAB, and the
693 resultant discrete time dynamic system (Equ. 4) was implemented by two integrating neuronal
694 populations representing $\hat{x}_k$ and $\hat{v}_k$, receiving a synaptic input on each time-step equal to:

695 $$\begin{bmatrix} \Delta\hat{x}_k \\ \Delta\hat{v}_k \end{bmatrix} = \begin{bmatrix} -K_{\text{pos}} & \Delta t \\ -K_{\text{vel}} & 0 \end{bmatrix}\begin{bmatrix} \hat{x}_{k-1} \\ \hat{v}_{k-1} \end{bmatrix} + \begin{bmatrix} K_{\text{pos}} \\ K_{\text{vel}} \end{bmatrix}y_k \qquad \text{(Equ. 16)}$$

696 Two LFP components were simulated by normalizing $\Delta\hat{x}_k$ and $\Delta\hat{v}_k$ to unity variance, before adding
697 background common noise with a $1/f$ spectrum.

698 The motor command u_k was generated on each time step using the Smith Predictor architecture
699 shown in Fig. 3F. Based on our observation that trajectory variability was maximal at times when force
700 output was changing (Figure S8), we used an linear quadratic regulator (LQR) control framework to
701 minimize a quadratic cost function, J, incorporating the rate of change in motor command, $\frac{\Delta u_k}{\Delta t}$:

702 $$J = \sum_k \left(qx_k{}^2 + r\left(\frac{\Delta u_k}{\Delta t}\right)^2 \right) \qquad \text{(Equ. 17)}$$

703 For a state transition matrix in the form:

704
$$\begin{bmatrix} x_k \\ v_k \end{bmatrix} = \begin{bmatrix} 1 & \Delta t \\ 0 & 1 \end{bmatrix} \begin{bmatrix} x_{k-1} \\ v_{k-1} \end{bmatrix} + \begin{bmatrix} 0 \\ 1 \end{bmatrix} \frac{\Delta u_k}{\Delta t}$$
(Equ. 18)

705 J is minimized by a state feedback policy of the form:

706
$$\frac{\Delta u_k}{\Delta t} = -\begin{bmatrix} K_I \\ K_P \end{bmatrix} \cdot \begin{bmatrix} x_k \\ v_k \end{bmatrix}$$
(Equ. 19)

707 which can be integrated to yield a PI controller:

708
$$u_k = \sum_{j=1}^k \Delta u_i$$

709
$$= -K_P \sum_{j=1}^k v_k \Delta t - K_I \sum_{j=1}^k x_j \Delta t$$

710
$$= -K_P x_k - K_I \sum_{j=1}^k x_j \Delta t$$
(Equ. 20)

711 We found the proportional and integral gains K_P and K_I using the function *lqr* in MATLAB with $q = 1$
712 and $r = \Delta t^2$. In the full model, this controller acted on the optimal estimate of position, $\hat{z}_k$, after
713 incorporating the delay feedback loop of the Smith Predictor. Note that the transfer function of a PI
714 controller inside the fast feedback loop of the Smith Predictor is given by (Abe and Yamanaka, 2003):

715
$$H_{PI}(i\omega) = \frac{K_P + K_I/i\omega}{1 + K_P + K_I/i\omega}$$
(Equ. 21)

716 which equals 1 for $\omega = 0$ but tends to $\frac{K_P}{1 + K_P}$ at higher frequencies. Therefore this effectively reduces
717 the response amplitude to perturbations. The full transfer function of the intrinsic dynamics, including
718 time-delay is given by:

719
$$H_{force}(i\omega) = e^{-i\omega(\tau_{int} + \tau_{ext})} H_{PI}(i\omega) . H_{y \to \hat{z}}(i\omega)$$
(Equ. 22)

720
$$H_{cursor}(i\omega) = 1 - H_{force}(i\omega)$$
(Equ. 23)

721 where $H_{y \to \hat{z}}(i\omega)$ is the transfer function of the Kalman filter relating delayed position measurement
722 to optimal position estimate.

723

724 **Data and software availability**

725 Datasets from the human and monkey experiments, sample analysis code and modelling associated
726 with this work are available on Dryad doi:10.5061/dryad.53sq7kn.

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792

793   **Supplemental Information**

794

795   **Table S1. The dependency of submovement period on feedback delay.** Shown in the table are the
796   gradients and intercepts of regression lines fitted to each harmonic group in Figure 1E. The time period of each
797   spectral peak was regressed against feedback delay. Shown in square brackets are 95% confidence intervals of
798   these values. Also shown is the estimated intrinsic time delay calculated using Equ. 1.

799

Harmonic (N)	Predicted slope = 2/N	Measured slope	Measured intercept (ms)	R^2	P	τ_{int} = Intercept*N/2
1	2	1.89 [1.69,2.09]	589 ms [539,638]	0.90	<0.00001	294 ms [270,319]
3	0.67	0.59 [0.53,0.65]	226 ms [211,242]	0.94	<0.00001	340 ms [316,362]
5	0.4	0.33 [0.22,0.45]	146 ms [106,185]	0.75	<0.00001	364 ms [266,463]

800
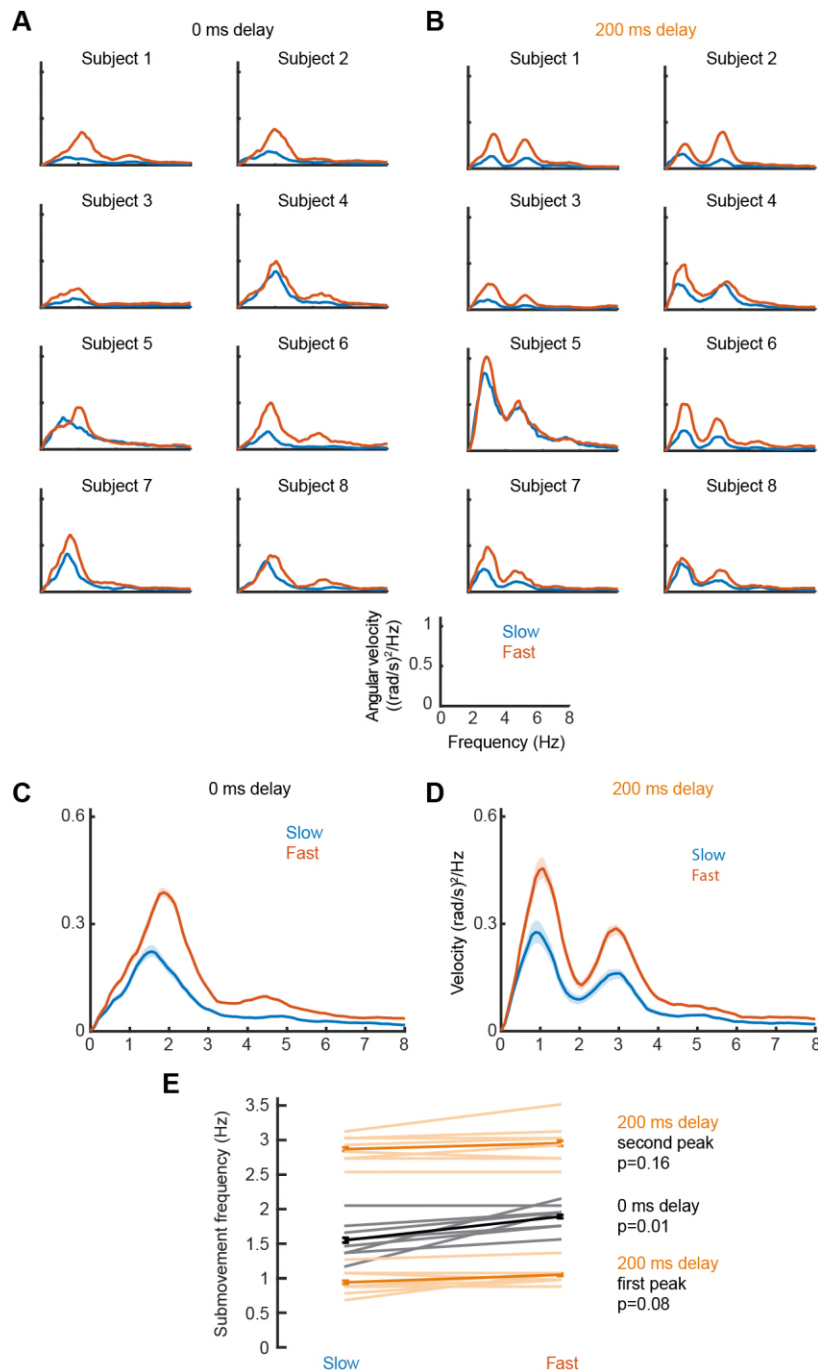
Figure S1. Effect of target speed on movement intermittency. (A) Power spectra of cursor angular velocity for individual subjects with slow (0.1 cycles/s) or fast (0.2 cycles/s) target rotation, and no feedback delay. (B) Power spectra of cursor angular velocity with slow or fast target rotation, and 200 ms feedback delay. (C,D) Average power, showing mean ± s.e.m. for 8 subjects. (E) Average ± s.e.m. frequencies of peak cursor velocity in each condition. P values calculated using a paired t-test.
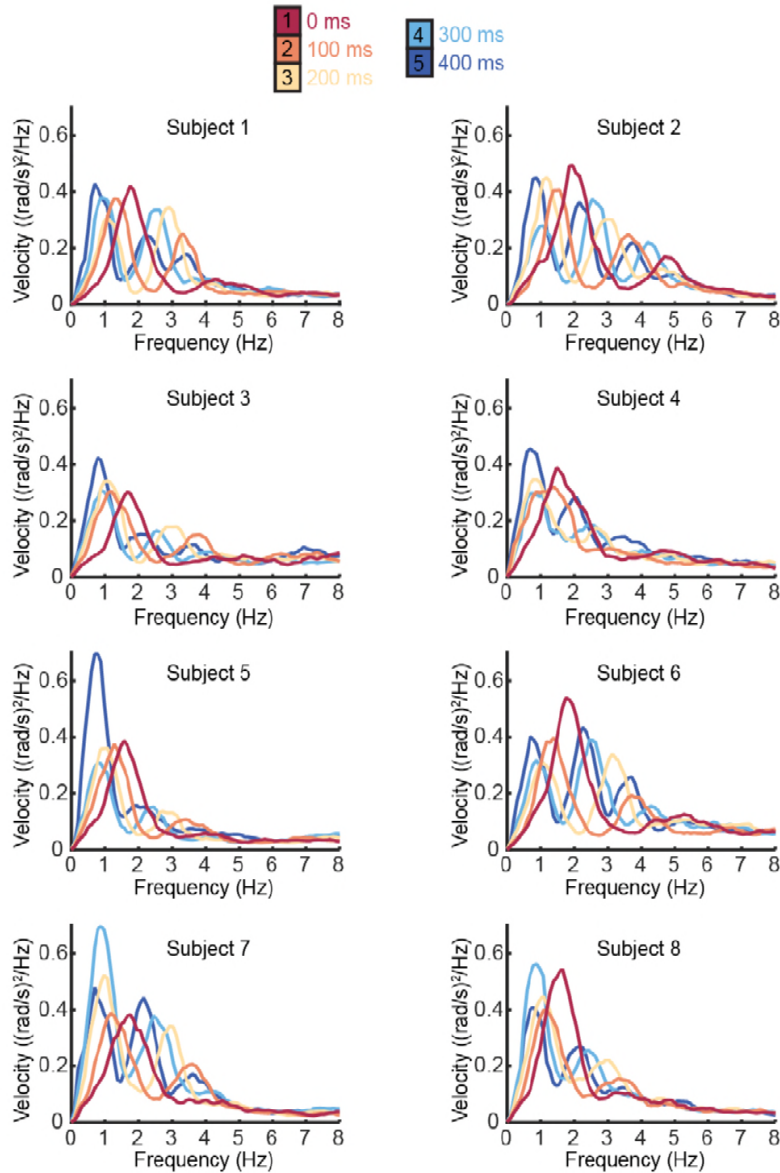
Figure S2. Individual subject power spectra of cursor velocity with different feedback delays. Power spectra of cursor angular velocity for individual subjects with 0–400 ms feedback delay. The average over subjects is shown in Figure 1D.
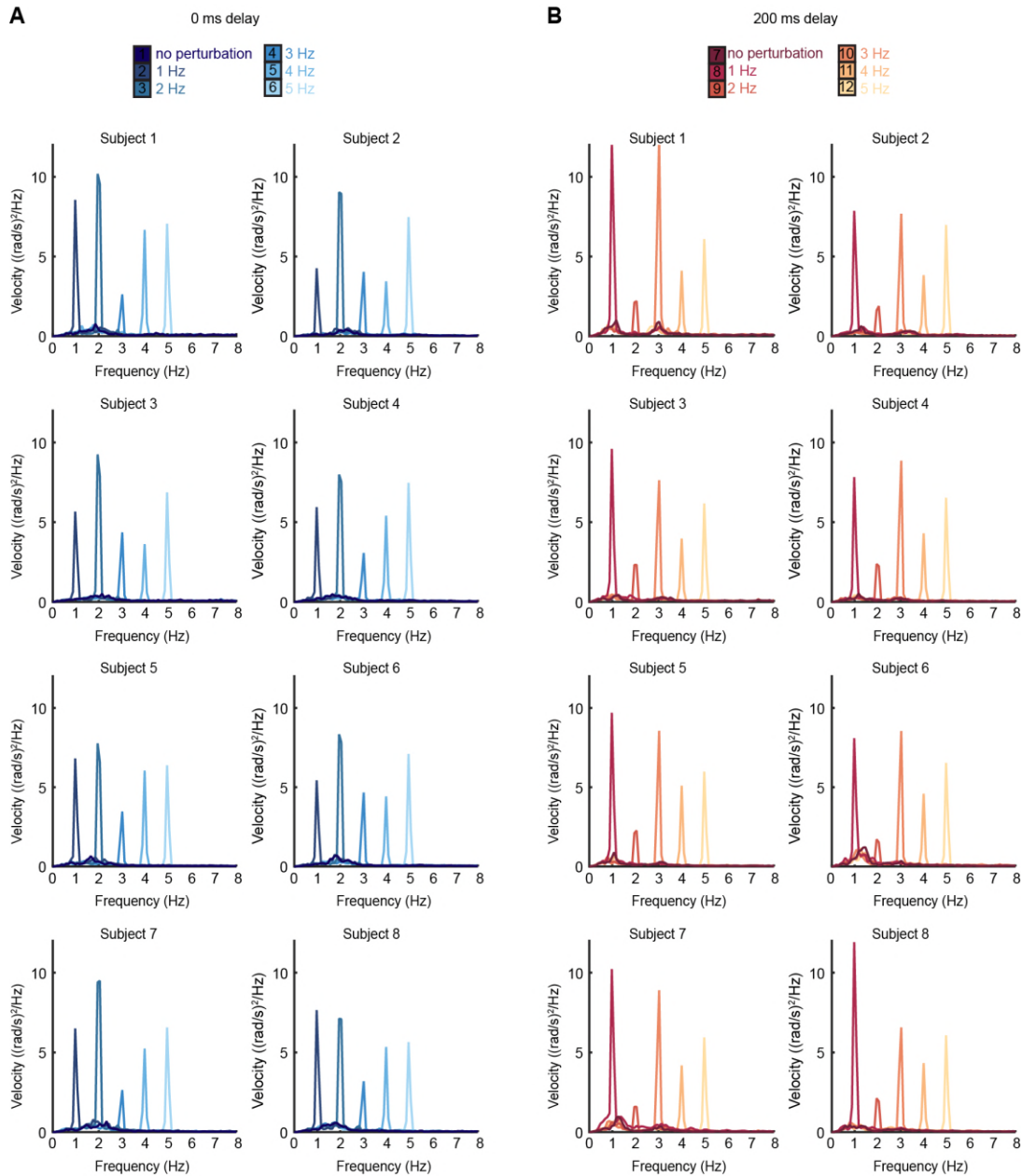
Figure S3. Individual subject power spectra of cursor velocity with perturbations. (A) Power spectra of cursor angular velocity for individual subjects with 1–5 Hz perturbations and no feedback delay. The average over subjects is shown in Figure 2C. (B) Power spectra of cursor angular velocity for individual subjects with 1–5 Hz perturbations and 200 ms feedback delay. The average over subjects is shown in Figure 2D.
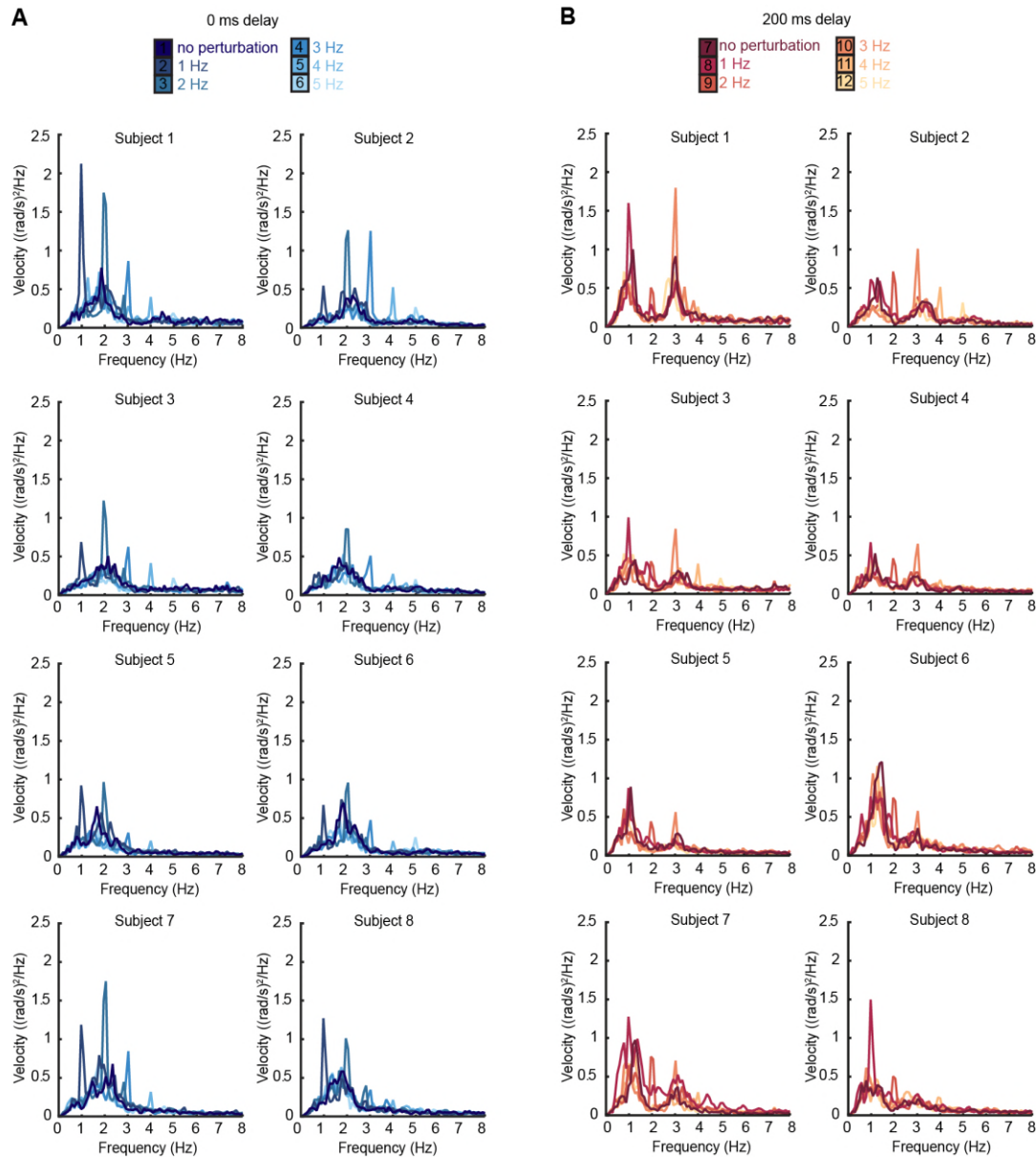
Figure S4. Individual subject power spectra of force velocity with perturbations. (A) Power spectra of force angular velocity for individual subjects with 1–5 Hz perturbations and no feedback delay. The average over subjects is shown in Figure 2F. (B) Power spectra of force angular velocity for individual subjects with 1–5 Hz perturbations and 200 ms feedback delay. The average over subjects is shown in Figure 2G.
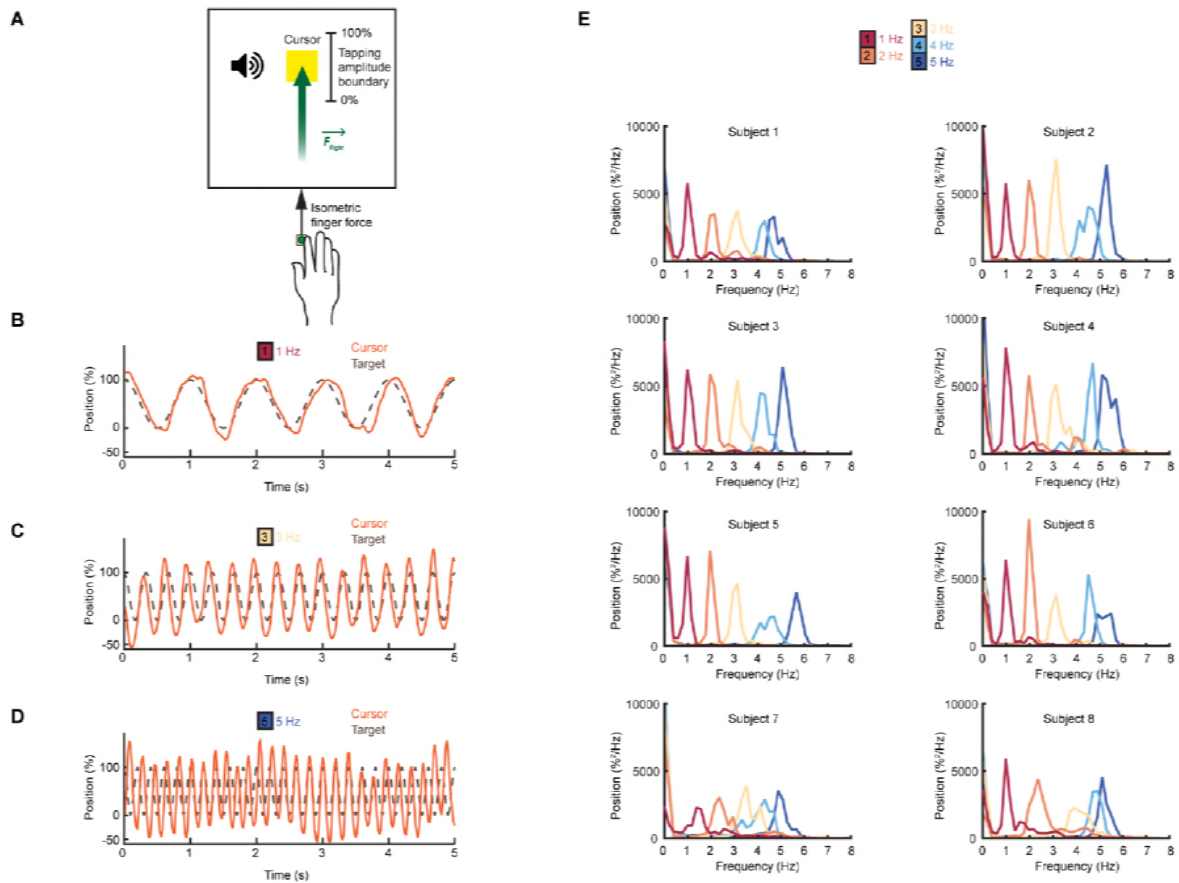
823

824 **Figure S5. Feedforward task.** (A) Schematic of the feedforward isometric task. Subjects generated
825 sinusoidal forces within a set range, at a frequency indicated by an auditory cue. (B-D) Performance
826 of an example subject for frequencies between 1-5 Hz. (E) Power spectrum of force for individual
827 subjects. The average over all subjects is shown in Figure 2J.
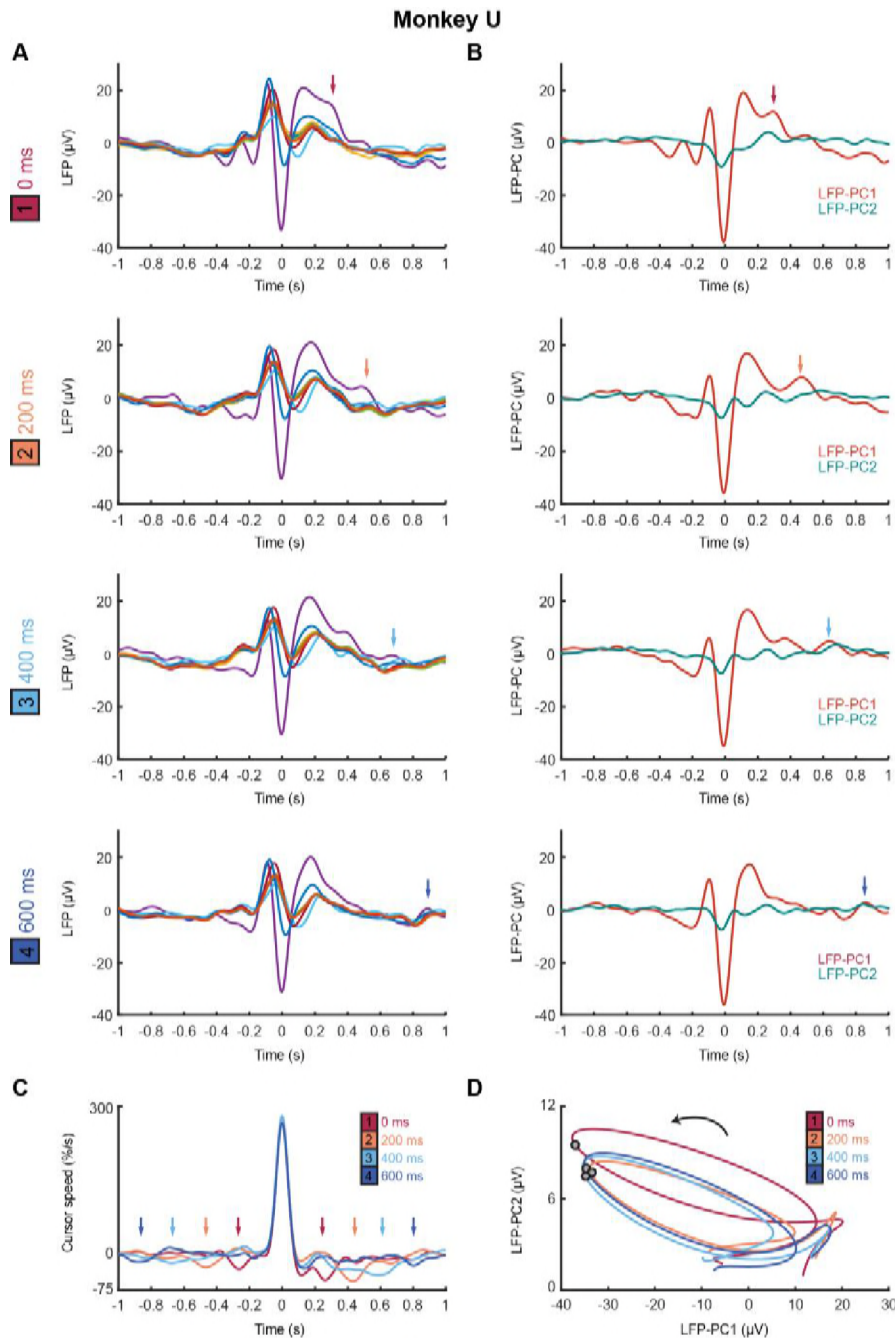
Figure S6. Submovement-triggered averages of M1 LFPs for Monkey U. (A) Average low-pass filtered LFPs from M1, aligned to the peak speed of submovements with 0–600 ms feedback delay. Arrows indicate second feature following submovement by an extrinsic delay-dependent latency. Data from Monkey U. (B) Average of first two LFP-PCs aligned to submovements. (C) Average low-pass filtered cursor speed, aligned to submovements. Arrows indicate symmetrical velocity troughs at extrinsic delay-dependent latencies. (D) Average submovement-triggered LFP-PC trajectories, plotted over 200 ms either side of the time of peak submovement speed (indicated by circles).
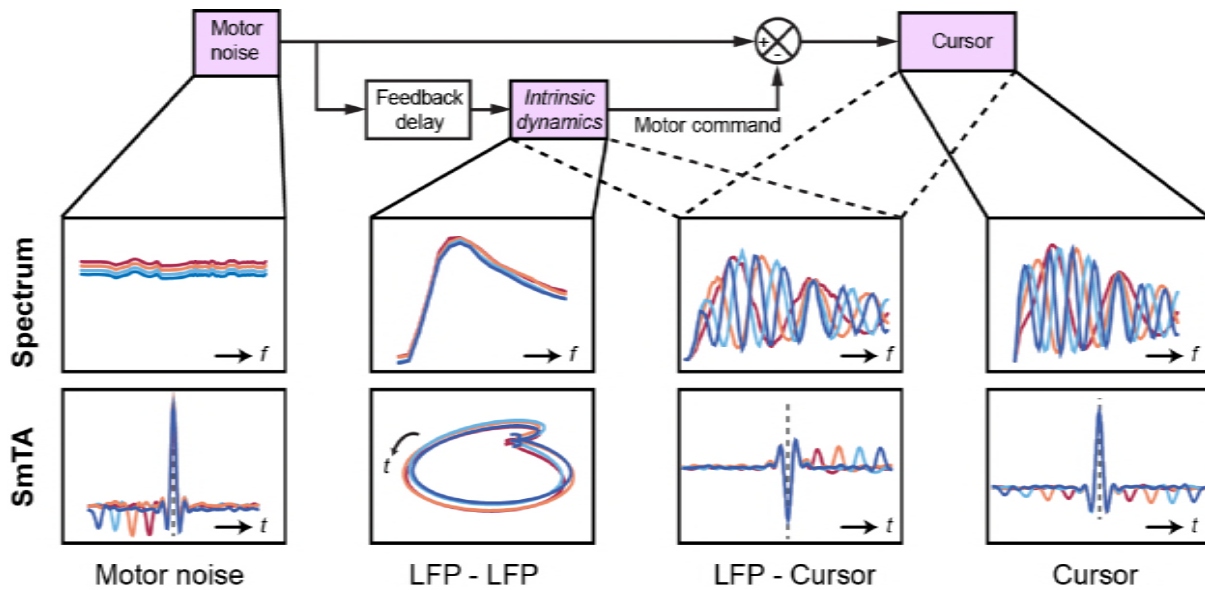
Figure S7. Schematic of delay-dependent and delay-independent relationships in OFC model. The boxes show how the various frequency-domain and submovement-triggered average (SmTA) relationships are explained by the OFC model. *Top row,* from left to right: Broad spectrum motor noise drives intrinsic dynamics resulting in a delay-independent LFP cross-spectral resonance. The delayed motor command is combined with the original motor noise leading to delay-dependent comb filtering evident in LFP-Cursor coherence and Cursor power spectrum. *Bottom row,* from left to right: submovements can arise from a positive noise peak at time-zero, or as a correction to a preceding negative noise trough. Due to intrinsic dynamics, LFPs trace consistent cyclical trajectories locked to submovements. SmTA of LFPs contains potentials associated with noise peak/troughs after feedback delay. SmTA of cursor velocity combines noise with delayed feedback corrections to yield a central submovement flanked by symmetrical troughs.
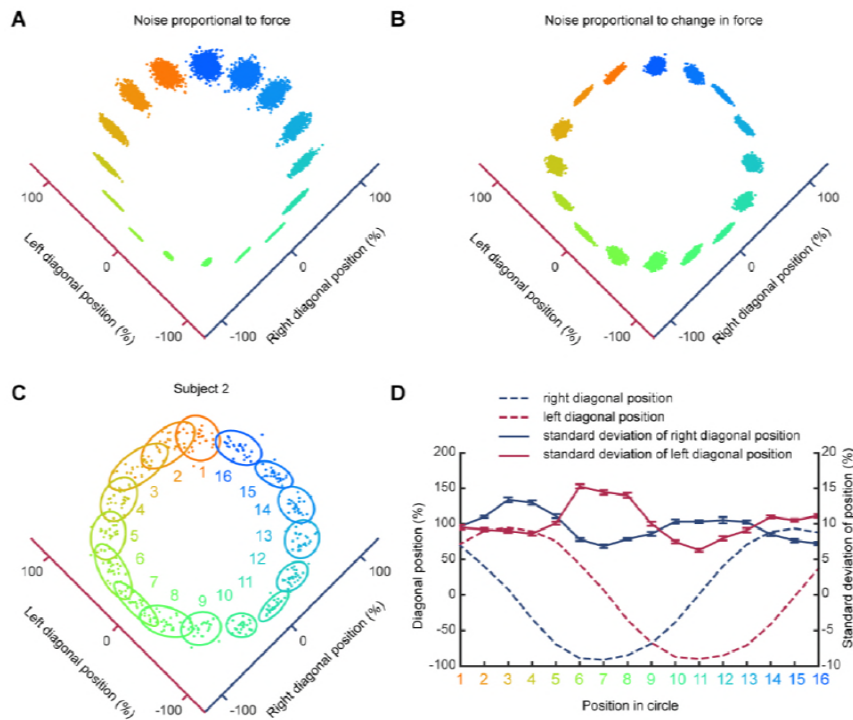
Figure S8. Trajectory variability depends on change in isometric force. (A) Simulated pattern of trial-to-trial variability if motor noise is proportional to absolute force. (B) Simulated pattern of trial-to-trial variability if motor noise is proportional to derivative of force. (C) Variability of a typical subject during counter clockwise tracking. 2D cursor position over multiple trials and associated covariance ellipses are shown for 16 target positions. (D) Average and s.e.m. of standard deviation of force along each finger axis for the 16 target positions. Note that variability is maximal at times of maximal change in associated finger force (*dashed lines*).

A ω_Cursor, ω_Target, r_{Cursor}, r_{Target}, F_{Left}, F_{Right}, Isometric finger force

B 1 0 ms delay
Position (%), F_{Left}, F_{Right}
Error (rad)
Angular velocity (rad/s)
Time (s)

C 5 400 ms delay
Position (%), F_{Right}, F_{Left}
Error (rad)
Angular velocity (rad/s)
Time (s)
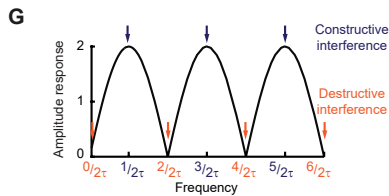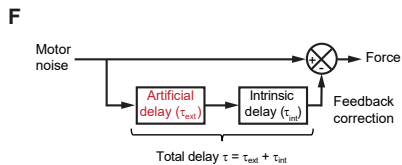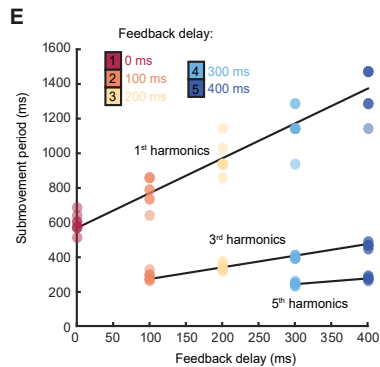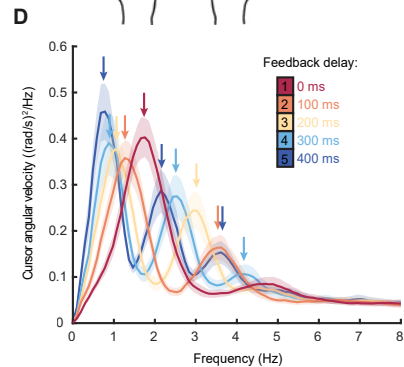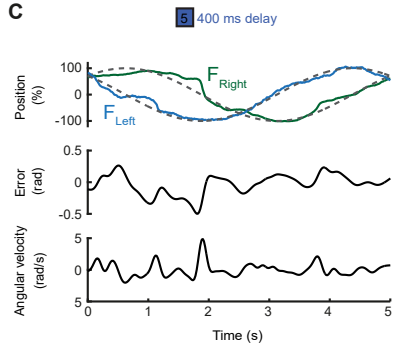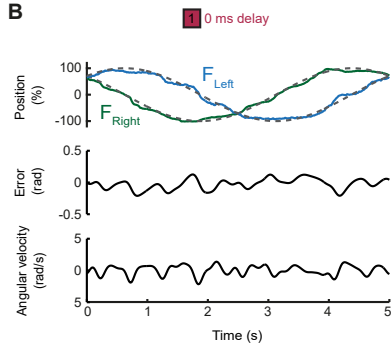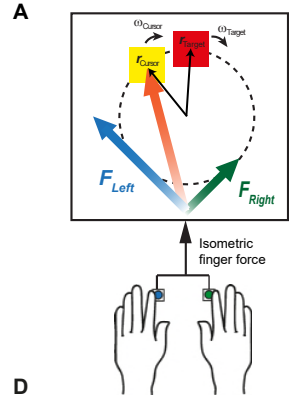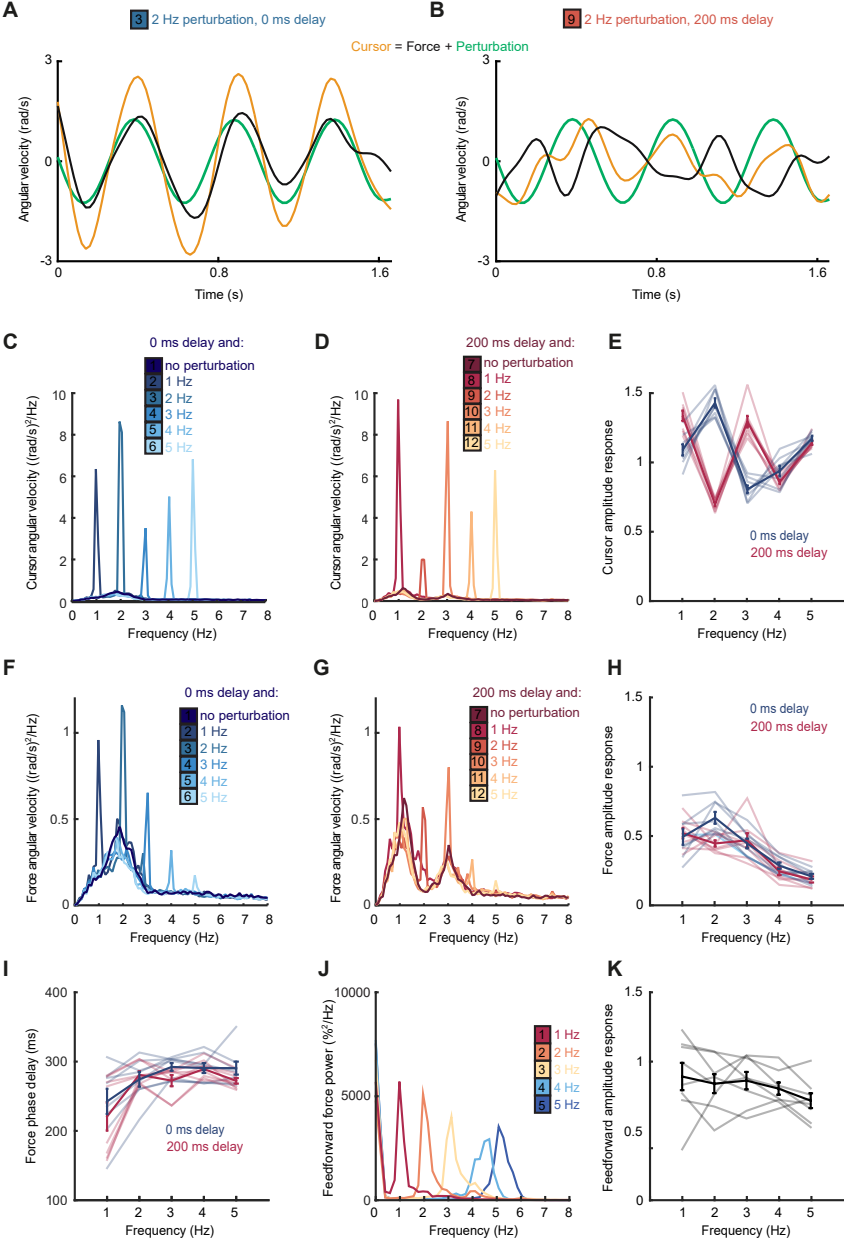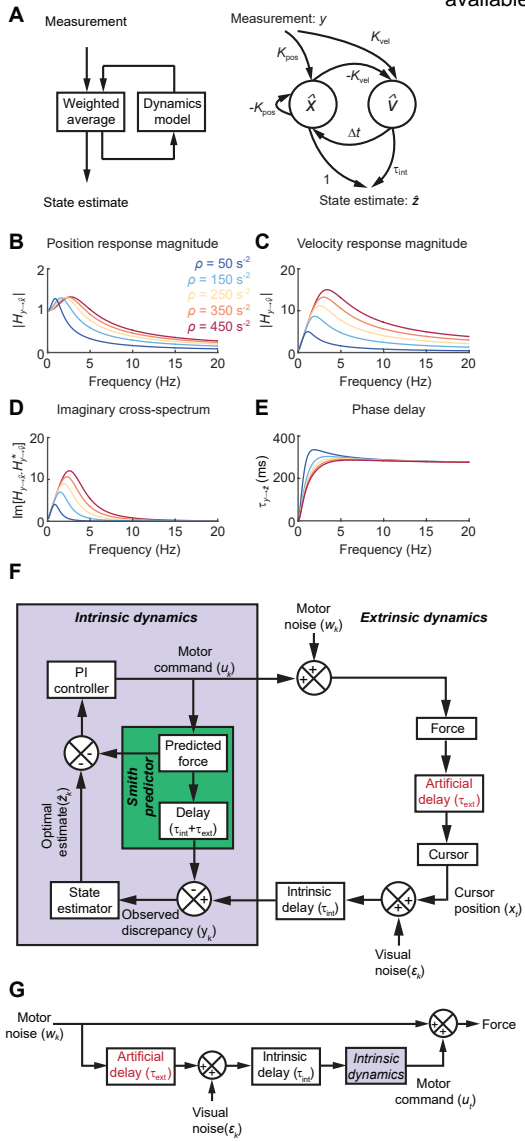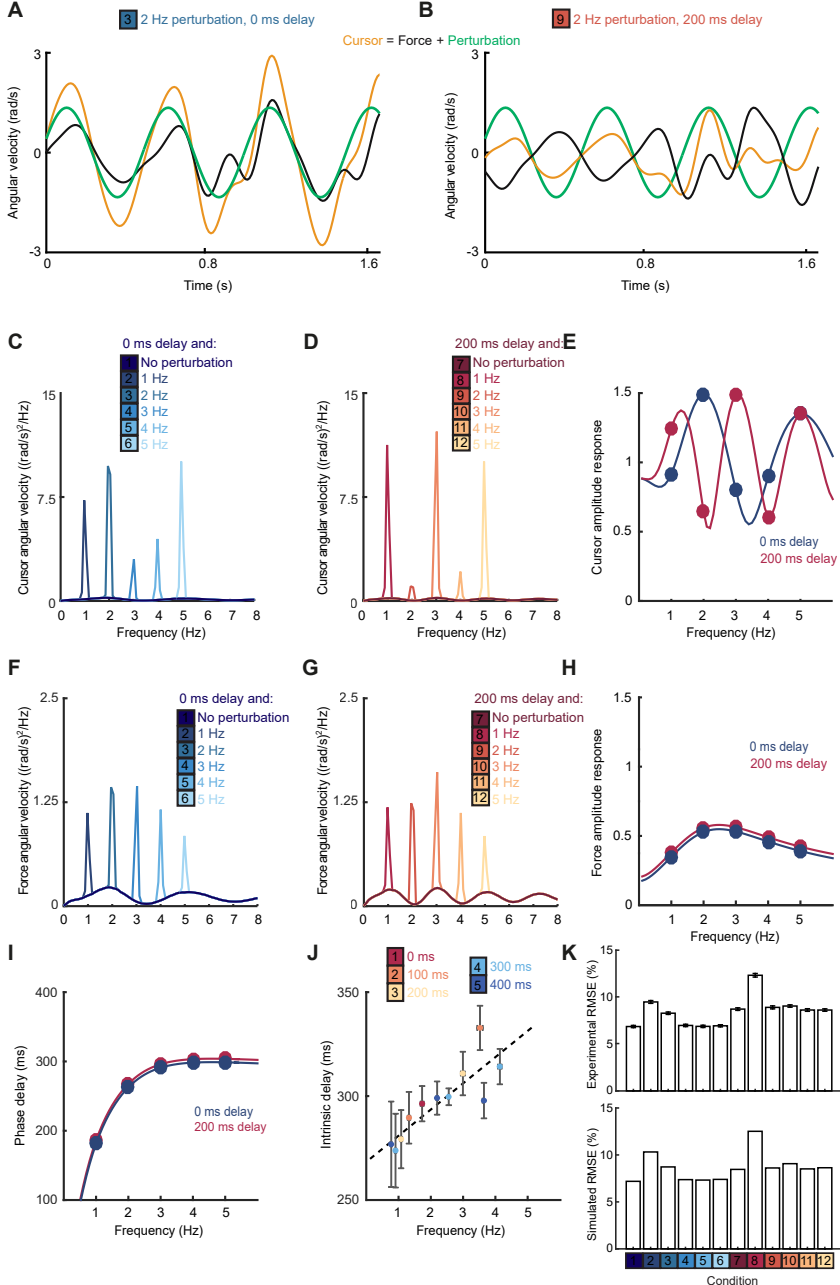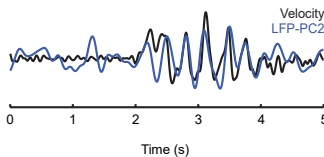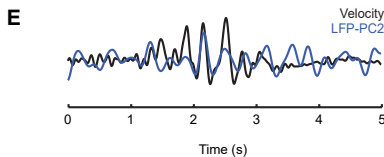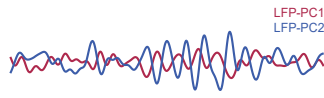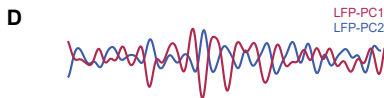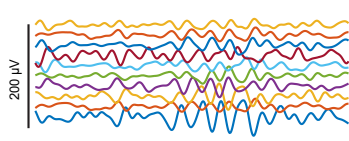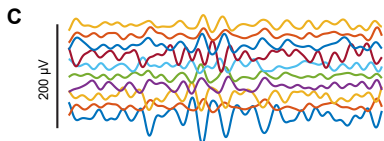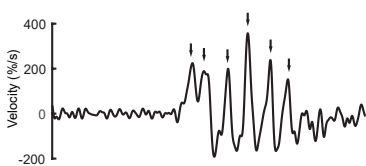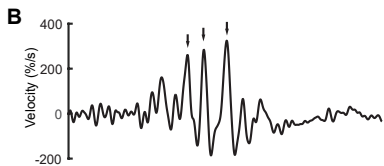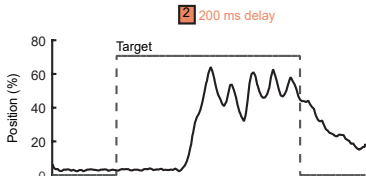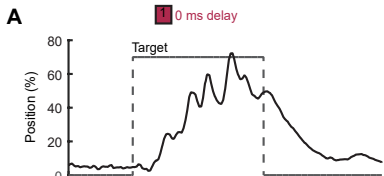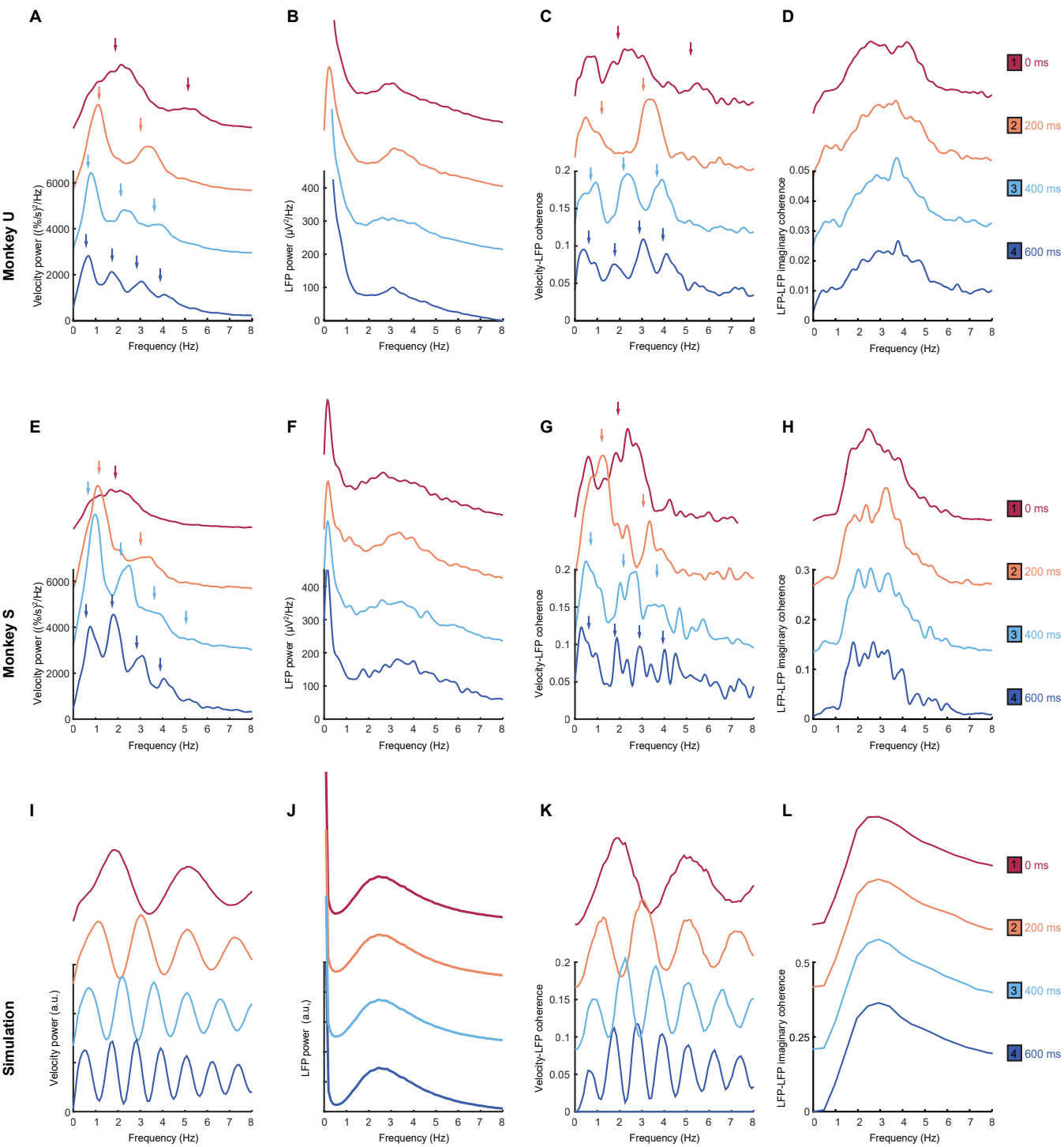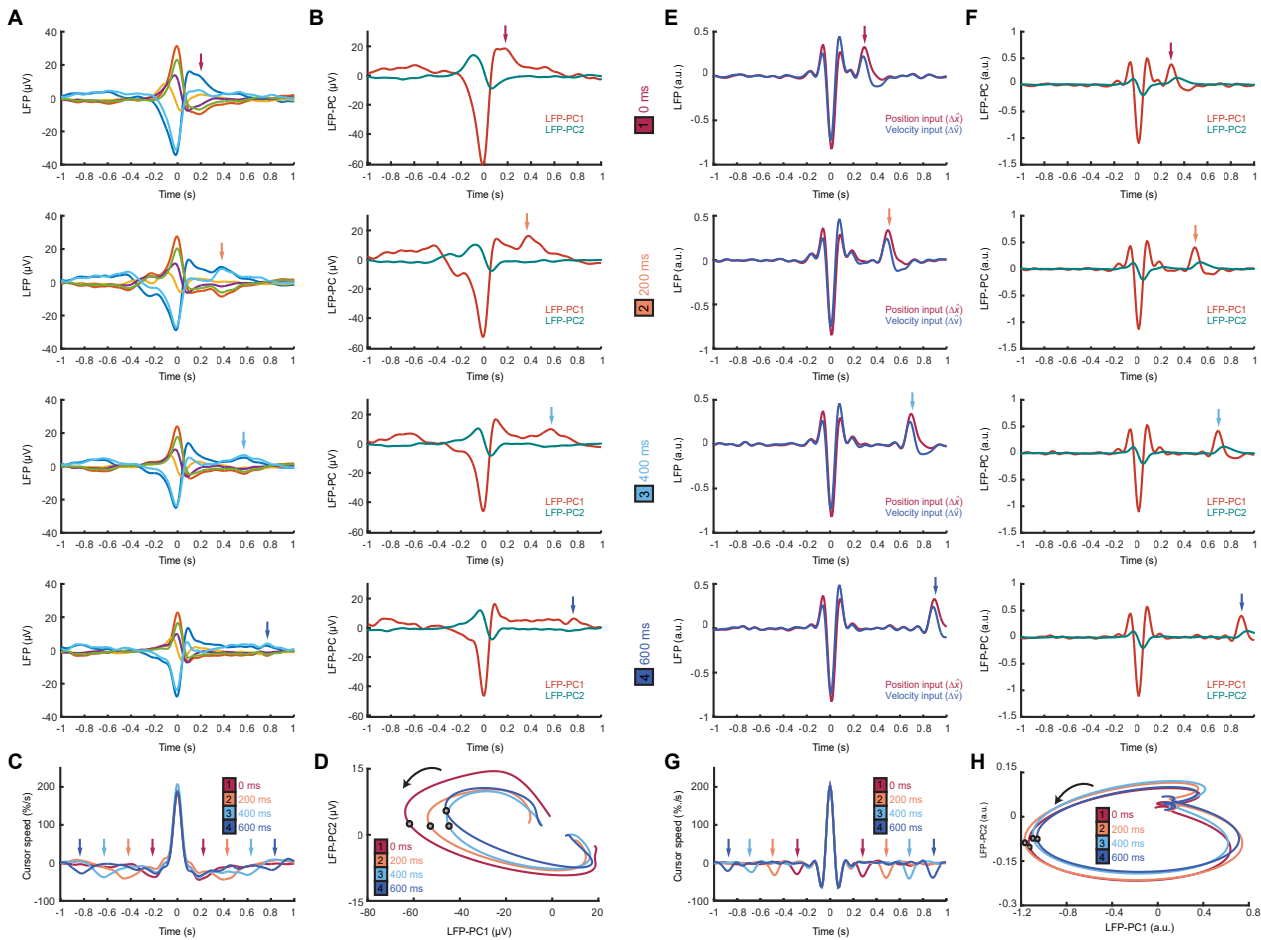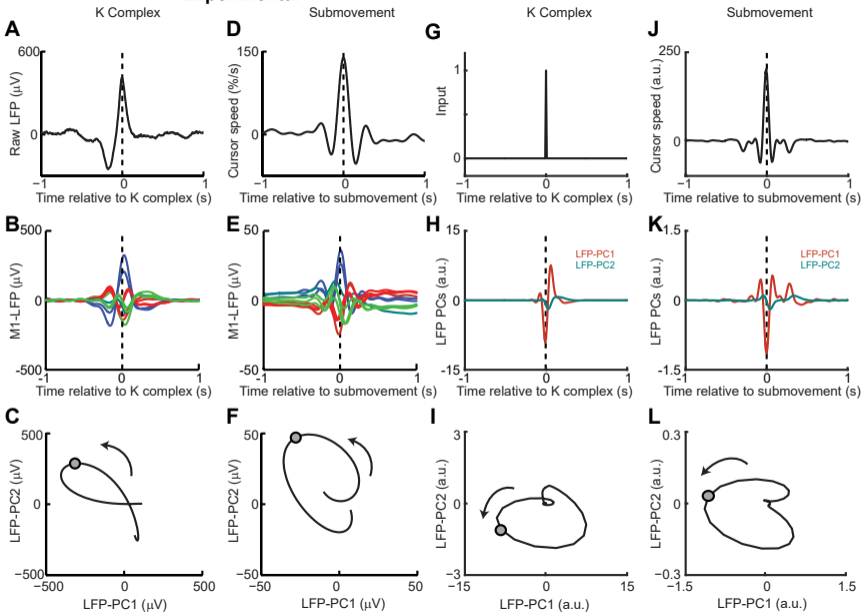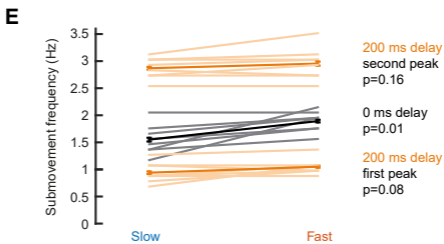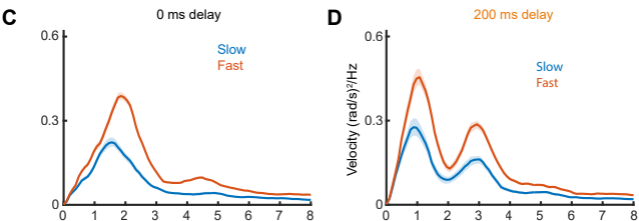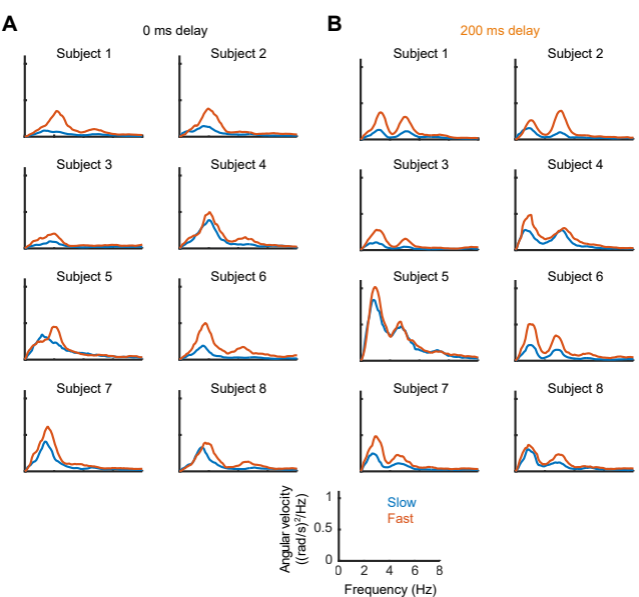
D Cursor angular velocity ((rad/s)²/Hz)
Feedback delay:
1 0 ms
2 100 ms
3 200 ms
4 300 ms
5 400 ms
Frequency (Hz)

E Submovement period (ms)
Feedback delay:
1 0 ms 4 300 ms
2 100 ms 5 400 ms
3 200 ms
1st harmonics
3rd harmonics
5th harmonics
Feedback delay (ms)

F Motor noise → Force
Artificial delay (τ_ext), Intrinsic delay (τ_int)
Feedback correction
Total delay τ = τ_ext + τ_int

G Amplitude response
Constructive interference
Destructive interference
$0/2\tau$ $1/2\tau$ $2/2\tau$ $3/2\tau$ $4/2\tau$ $5/2\tau$ $6/2\tau$
Frequency

A

B Position response magnitude

C Velocity response magnitude

$\rho = 50\ s^{-2}$
$\rho = 150\ s^{-2}$
$\rho = 250\ s^{-2}$
$\rho = 350\ s^{-2}$
$\rho = 450\ s^{-2}$

D Imaginary cross-spectrum

E Phase delay

F

G

A 2 Hz perturbation, 0 ms delay

Cursor = Force + Perturbation

B 2 Hz perturbation, 200 ms delay

C 0 ms delay and:
No perturbation
1 Hz
2 Hz
3 Hz
4 Hz
5 Hz

D 200 ms delay and:
No perturbation
1 Hz
2 Hz
3 Hz
4 Hz
5 Hz

E
0 ms delay
200 ms delay

F 0 ms delay and:
No perturbation
1 Hz
2 Hz
3 Hz
4 Hz
5 Hz

G 200 ms delay and:
No perturbation
1 Hz
2 Hz
3 Hz
4 Hz
5 Hz

H
0 ms delay
200 ms delay

I
0 ms delay
200 ms delay

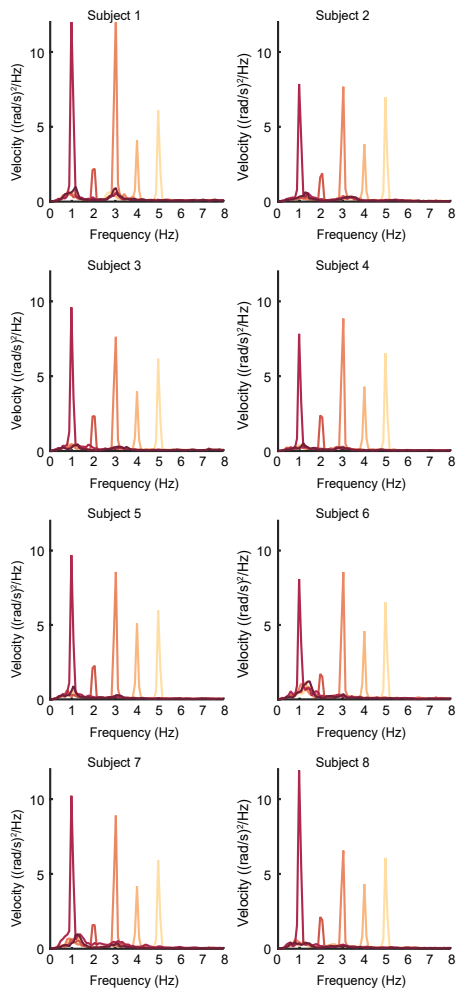**J**
0 ms
100 ms
200 ms
300 ms
400 ms

K

A

Target

1 0 ms delay

2 200 ms delay

Target

B

C

200 µV

200 µV

D

LFP-PC1
LFP-PC2

LFP-PC1
LFP-PC2

E

Velocity
LFP-PC2

Velocity
LFP-PC2

Time (s)

Time (s)

Monkey S   **Simulation**

Experimental

K Complex

A
Raw LFP (μV)
Time relative to K complex (s)

B
M1-LFP (μV)
Time relative to K complex (s)

C
LFP-PC2 (μV)
LFP-PC1 (μV)

Submovement

D
Cursor speed (%/s)
Time relative to submovement (s)

E
M1-LFP (μV)
Time relative to submovement (s)

F
LFP-PC2 (μV)
LFP-PC1 (μV)

Simulation

K Complex

G
Input
Time relative to K complex (s)

H
LFP PCs (a.u.)
LFP-PC1
LFP-PC2
Time relative to K complex (s)

I
LFP-PC2 (a.u.)
LFP-PC1 (a.u.)

Submovement

J
Cursor speed (a.u.)
Time relative to submovement (s)

K
LFP PCs (a.u.)
LFP-PC1
LFP-PC2
Time relative to submovement (s)

L
LFP-PC2 (a.u.)
LFP-PC1 (a.u.)

A 0 ms delay

Subject 1 Subject 2
Subject 3 Subject 4
Subject 5 Subject 6
Subject 7 Subject 8

B 200 ms delay

Subject 1 Subject 2
Subject 3 Subject 4
Subject 5 Subject 6
Subject 7 Subject 8

Angular velocity ((rad/s)²/Hz)

Slow
Fast

Frequency (Hz)

C 0 ms delay

Slow
Fast

D 200 ms delay

Velocity (rad/s)²/Hz

Slow
Fast

E

Submovement frequency (Hz)

200 ms delay
second peak
p=0.16

0 ms delay
p=0.01

200 ms delay
first peak
p=0.08

Slow   Fast

A 0 ms delay

- ■ no perturbation
- 2 1 Hz
- 3 2 Hz
- 4 3 Hz
- 5 4 Hz
- 6 5 Hz

B 200 ms delay

- 7 no perturbation
- 8 1 Hz
- 9 2 Hz
- 10 3 Hz
- 11 4 Hz
- 12 5 Hz

Subject 1 — Subject 8 (columns A and B), plots of Velocity ((rad/s)²/Hz) versus Frequency (Hz).

A 0 ms delay

2 1 Hz   no perturbation   4 3 Hz
3 2 Hz   5 4 Hz
   6 5 Hz

B 200 ms delay

7 no perturbation   10 3 Hz
8 1 Hz   11 4 Hz
9 2 Hz   12 5 Hz

Monkey U

	Motor noise	LFP - LFP	LFP - Cursor	Cursor
Spectrum				
SmTA				

A Noise proportional to force

B Noise proportional to change in force

Left diagonal position (%) — 100, 0, -100
Right diagonal position (%) — 100, 0, -100

C Subject 2

1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16

Left diagonal position (%) — 100, 0
Right diagonal position (%) — 0, 100, -100

D

- - - right diagonal position
- - - left diagonal position
——— standard deviation of right diagonal position
——— standard deviation of left diagonal position

Diagonal position (%): 200, 150, 100, 50, 0, -50, -100
Standard deviation of position (%): 20, 15, 10, 5, 0, -5, -10

Position in circle: 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16