

Cyclic, condition-independent activity in primary motor cortex predicts corrective movement behavior

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1 **Title:** Cyclic, condition-independent activity in primary motor cortex predicts corrective movement
2 behavior

3 **Abbreviated Title:** Cyclic neural activity in corrective movements

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26

27 **Abstract**

28 Reaching movements are known to have large condition-independent neural activity and cyclic
29 neural dynamics. A new precision center-out task was performed by rhesus macaques to test the
30 hypothesis that cyclic, condition-independent neural activity in the primary motor cortex (M1) occurs not
31 only during initial reaching movements but also during subsequent corrective movements. Corrective
32 movements were observed to be discrete with time courses and bell-shaped speed profiles similar to the
33 initial movements. Condition-independent cyclic neural trajectories were similar and repeated for initial
34 and each additional corrective submovement. The phase of the cyclic condition-independent neural
35 activity predicted the time of peak movement speed more accurately than regression of instantaneous
36 firing rate, even when the subject made multiple corrective movements. Rather than being controlled as
37 continuations of the initial reach, a discrete cycle of motor cortex activity encodes each corrective
38 submovement.

39 **Significance Statement**

40 During a precision center-out task, initial and subsequent corrective movements occur as discrete
41 submovements with bell-shaped speed profiles. A cycle of condition-independent activity in primary
42 motor cortex neuron populations corresponds to each submovement, such that the phase of this cyclic
43 activity predicts the time of peak speeds—both initial and corrective. These submovements accompanied
44 by cyclic neural activity offer important clues into how we successfully execute precise, corrective
45 reaching movements and may have implications for optimizing control of brain-computer interfaces.

46 **Introduction**

47 Corrective movements based on sensorimotor feedback are critical for elegant motor control.
48 While a single, discrete movement like a pointing gesture may be mostly ballistic, more precise aiming
49 movements typically require an error correction phase (Woodworth, 1899; Craik, 1947; Abrams et al.,
50 1990; Sainburg et al., 1999; Elliott et al., 2010). In making an online correction, the brain must respond

51 to updated sensory information about the current position relative to the desired target. Yet the way
 52 neurons in motor areas of the brain encode and generate corrective movements to achieve movement
 53 precision is relatively unexplored. When examining populations of neurons in primary motor cortex
 54 during instructed movements, predictable dynamics of neural spiking occur with a progression from
 55 initiation to completion of a movement (Maynard et al., 1999; Jackson et al., 2003; Truccolo et al., 2005;
 56 Sarma et al., 2010). Yet behaving animals also respond to updated sensorimotor information, as happens
 57 in tasks that require precision. For corrective movements with new sensory information, does the neural
 58 activity update within a current active neural state as a continuation of the initial reach or does it repeat
 59 and cycle again through the same series of neural dimensions for each additional submovement?

60 We investigated the neural dynamics underlying corrective movements, focusing on two key
 61 features of neural activity in primary motor cortex that have been previously described during reaching: i)
 62 condition-independent neural activity and ii) rotations in neural dynamics. Although individual neurons
 63 in primary motor cortex encode a variety of condition-dependent movement features (Evarts, 1968;
 64 Thach, 1978; Georgopoulos et al., 1982; Kalaska et al., 1989; Kakei et al., 1999), there is also a large
 65 condition-independent component in the firing rate of neurons in motor cortex (Kaufman et al., 2016;
 66 Rouse and Schieber, 2018). Condition-independent neural activity is the change in a neuron's firing rate
 67 from baseline over time that happens regardless of the instructed movement for any given trial within a
 68 given task. Condition-independent activity presumably carries information on the timing of movement as
 69 opposed to specific, condition-dependent features. Techniques like demixed principal component
 70 analysis can partition a neural population's activity into condition-independent modulation and the more
 71 classically described condition-dependent tuning to task conditions (Kobak et al., 2016). In addition to
 72 being condition-independent or -dependent, changes in firing rate in theory might be temporally
 73 synchronous across a population. But in practice, primary motor cortex neurons have an asynchronous
 74 range of onset latencies before movement, with latencies for most corticomotoneuronal (CM) cells
 75 ranging from 120ms to 0ms (Cheney and Fetz, 1980) while other motor cortex neurons can lead

76 movement by up to 200ms (Moran and Schwartz, 1999). Because the increases and decreases in firing
 77 rates are not synchronous, the population activity forms a more complex trajectory in neural state space
 78 (Yu et al., 2007; Cunningham and Yu, 2014). These time-varying dynamics can either be dependent on
 79 specific task conditions or independent of task conditions. While the precise meaning of these features of
 80 neural dynamics under different conditions remains debated (Churchland et al., 2012; Hall et al., 2014;
 81 Michaels et al., 2016; Lebedev et al., 2019), these shifts between different combinations of active neurons
 82 leads to changing dimensions of the neural space.

83 We hypothesized that if the primary motor cortex handles online corrections as ongoing
 84 adjustments to a single reach, then one cycle of the neural trajectory would include both the initial and the
 85 corrective submovements. In contrast, if the primary motor cortex handles each correction as a distinct
 86 (albeit smaller) movement, then each corrective submovement would correspond to its own cycle
 87 repeating the series of neural dimensions that are traversed. We used a precision center-out task that
 88 required moving to small targets (either narrow or shallow) to elicit visuomotor corrections. We
 89 examined whether corrective movements in this task were simple adjustments in the ongoing reach or
 90 discrete submovements, behaviorally similar to initial movements. We then ask whether condition-
 91 independent activity—representing the time course of movement irrespective of its direction or
 92 amplitude—is similar for both initial and corrective submovements. Finally, we ask whether cyclic
 93 neural dynamics improve our predictions of when initial and corrective movements occur.

94 **Materials and Methods**

95 *Non-human primates*

96 Two male rhesus monkeys, P and Q (weight 11 and 10 kg, ages 7 and 6 years old, respectively),
 97 were subjects in the present study. All procedures for the care and use of these nonhuman primates
 98 followed the Guide for the Care and Use of Laboratory Animals and were approved by the University
 99 Committee on Animal Resources at the University of Rochester Medical Center, Rochester, NY.

100 *Experimental Design*

101 A precision center-out task was performed by the monkey, using an 18 cm handle attached to a
102 commercial joystick (M212 series joystick, PQ Controls Inc.) to control a cursor on a 24" LCD display.
103 The joystick handle moved freely with minimal resistance as the spring mechanism for providing
104 centering, restorative force was removed. The end of the joystick could move approximately 9.3 cm in
105 both the forward/backward and left/right directions. Motion of the joystick was transduced linearly by
106 two Hall effect sensors sliding in both the backward/forward and left/right directions. The cursor viewed
107 by the monkey directly represented the planar position of these two sensors scaled to fit within a 1000
108 horizontal x 1000 vertical pixel workspace in the center of the LCD display. The limits of the cursor
109 workspace were slightly within the physical limits of the joystick, with 110 pixels corresponded to
110 approximately 1 cm of movement at the end of the joystick. The cursor appeared on the display as a
111 small cross centered on a single pixel in the workspace. Custom software for task control sampled the
112 joystick data, updated the scene, and stored the cursor position (equivalent to joystick position) and trial
113 event times at 100 Hz.

114 The precision center-out task consisted of three sets of eight peripheral targets located
115 equidistance and equally spaced in 45° intervals around a center, home target (see Figure 2). The center
116 target had a radius of 75 pixels. Each center-out target—defined in polar coordinates—was one of three
117 different sizes i) large targets spanning 45° of the workspace and covering 250-450 pixels from the center,
118 ii) shallow targets spanning 45° but covering a width of only 325-375 pixels from the center, and iii)
119 narrow targets spanning 15° covering 250-450 pixels from the center. All 24 targets (3 sizes x 8
120 locations) were presented pseudo-randomly in equal amounts throughout a session.

121 For each trial, following the subject acquiring the home target and performing a required initial
122 hold ranging from 300-500 ms, the instruction occurred with the given trial's correct target changing from
123 black to green. Following this instruction, the monkey could move the cursor immediately to contact the
124 correct target. At contact, the outline of all targets changed colors from white to black providing visual

125 feedback that the cursor was within the target boundaries. After contacting the desired target, the cursor
 126 was required to remain within the target for a variable hold time of 500-600 ms. If the cursor left the
 127 target during this hold, the monkey was allowed to enter the target again and complete a final hold. Once
 128 a successful final hold of 500-600 ms was completed, the animal received a liquid reward. Both the
 129 required initial and final hold times for each trial were randomly sampled from a uniform distribution.

130 *Neural Recordings*

131 Floating microelectrode arrays (MicroProbes for Life Science) were implanted in the anterior lip
 132 and bank of the central sulcus to record from primary motor cortex (M1) in each monkey, using methods
 133 described in detail previously (Mollazadeh et al., 2011; Rouse and Schieber, 2016). For monkey P,
 134 recordings were collected from six 16-channel arrays implanted in M1. For monkey Q, two 32-channel
 135 arrays and one 16-channel array in M1 were used. The location of the implanted arrays, spanning the
 136 forelimb representation in M1, have been previously reported (Fig. 2 of (Liu and Schieber, 2020)) and
 137 spanned the forelimb area of M1. Intracortical microstimulation on single electrodes with a current up to
 138 a maximum of 100 μ A (12 biphasic pulses, 0.2ms pulse width per phase, 3ms interpulse interval) with the
 139 animal lightly anesthetized with ketamine evoked a variety of forelimb movements. Of the 96 electrodes
 140 for monkey P, stimulation of 11 sites elicited proximal arm movements, 6 sites elicited wrist movements,
 141 and 21 sites elicited movement of the digits. Of the 80 electrodes for monkey Q, 34 sites were proximal,
 142 9 sites were wrist, and 25 were digits. During recording sessions, channels with spiking activity were
 143 thresholded manually online, and spike-waveform snippets and spike times were collected with Plexon
 144 MAP (Plexon, Inc.) and Cerebus (Blackrock Microsystems, LLC.) data acquisition systems. The spike
 145 snippets were sorted off-line with a custom, semi-automated algorithm. Chronic multielectrode arrays do
 146 not always yield well-isolated single-unit recordings. To define likely single units, we utilized the signal
 147 to noise ratio of the sorted spike waveforms and the percent of true single unit spikes estimated from a
 148 formula using the number of interspike interval (ISI) violations less than 1ms (Hill et al., 2011; Rouse and
 149 Schieber, 2016). Using a signal to noise ratio of $SNR > 3$ and 100% true single unit spikes (no ISI

violations) to define definite single units and $\text{SNR} > 2.5$ and $>90\%$ true single unit spikes to define probable single units, 543 (monkey P) and 304 (monkey Q) of sorted spike waveforms were classified as definite single units while 268 (P) and 208 (Q) additional units were probable single units. Thus, $811/1293=63\%$ (monkey P) and $512/1185 = 43\%$ (monkey Q) of all spiking units were classified as likely single units. Because the estimation of neural population states from multi-unit activity has previously been shown to be quite similar to that from well isolated single units (Trautmann et al., 2019) and because including multi-units would be unlikely to provide results more significant than similar numbers of single-units, we included both single- and multi-unit recordings in our analyses.

Behavior Analyses

A peak finding algorithm to identify local maxima was used for analysis of the timing of cursor speed peaks. Off-line, cursor speed was calculated by filtering the cursor position with a 10-Hz low-pass 1st-order Butterworth filter (bidirectionally for zero phase lag) and then calculating the first derivative using the 5-point central difference. Local maxima of cursor speeds (identified with *findpeaks* function in Matlab (Mathworks, 2020)) were identified as peaks if they met the following criteria: i) the peak speed was greater than 250 pixels/s and ii) the peak's prominence—the height difference between the peak and the larger of the two adjacent troughs (minimum speed before encountering a larger peak)—was at least 50% of the absolute height of the peak. All such cursor speed peaks with their surrounding ± 200 ms time windows were considered submovements within a trial. Initial peaks were identified as the first submovement that ended at least 150 pixels from the center (approximately halfway to the peripheral target). Any small movements before the initial speed peak—506 (4.6% of trials) for P and 616 (7.0% of trials) for Q—were discarded from further analysis. Speed peaks following the initial speed peak were defined as corrective submovements. To focus analysis on submovements made to successfully acquire the target, corrective submovements were only included if some portion of the acceleration phase—time from preceding speed trough to speed peak—occurred outside the peripheral target.

174 The speed profiles for individual submovements were analyzed between -200 and 200 ms relative
 175 to peak speed. As a measure of similarity between speed profiles, the Pearson's correlation between these
 176 speed profiles for pairs of submovements was calculated, yielding a similarity score between -1 and 1. To
 177 measure how similar corrective submovements were to initial submovements, the correlation of each
 178 initial submovement to a randomly selected corrective submovement was calculated. As a ceiling
 179 comparison, each initial submovement was also compared to another randomly selected initial
 180 submovement. Thus, the distribution of correlations for initial-corrective submovement pairs was
 181 compared to the distribution of initial-initial pairs.

182 *Identifying condition-independent, rotational neural activity*

183 We focused our neural population analysis on the neural dimensions that contained the most
 184 condition-independent, rotational activity. A schematic illustration of these two features—i) condition-
 185 independent vs. -dependent, and ii) synchronous vs. rotational/asynchronous is shown in Figure 1. The
 186 condition-independent activity is the time-varying average of firing rate across all trials regardless of
 187 condition while the condition-dependent is the specific tuning to task condition like target direction.
 188 Synchronous, time-locked activity represents changes in firing rate that happen simultaneously across the
 189 neural population, while asynchronous activity of varying time course in different neurons can lead to
 190 patterns of traveling waves or oscillations in the population with a predictable progression in time.

191 Firing rates of the neural population can be visualized as either: i) a function of time (Fig. 1B) or
 192 ii) neural trajectories in a Cartesian neural space where each neuron's firing rate is plotted on an
 193 orthogonal dimension (Fig. 1C). For a complex task with variable corrective submovements such as our
 194 precision center-out task, the condition-independent activity provides a useful analysis to identify the
 195 neural activity underlying a submovement. Although a synchronous rise and fall of firing rate across the
 196 neural population—a single neural dimension—may provide some information, utilizing additional neural
 197 dimensions of the condition-independent signal may help improve our prediction of the timing and phase
 198 of submovements. The simplest is to consider two-dimensions of condition-independent activity in which

199 the rotational activity resulting from sequential firing rate changes across different neurons produces a
 200 cycle in a neural plane. This approach has the potential to improve identification of corrective
 201 submovements.

202 <Insert Figure 1 near here>

203 *Dynamical Systems Model*

204 Traditionally, condition-independent signals are identified by aligning neural data to behavioral
 205 cues and time averaging with methods like dPCA (Kaufman et al., 2016; Ames and Churchland, 2019).
 206 However, our precision center-out task consisted of corrective movements that were highly variable in
 207 their timing relative to any experimental controlled behavioral event. We therefore employed dynamical
 208 system modeling to characterize repeated changes in firing rates across our recorded neural population.
 209 To identify and analyze potential repeatable temporal dynamics of the neural population that correlated
 210 with movement, our neural data was modeled as a linear, time-invariant system using a system of coupled
 211 first-order ordinary differential equation defined by a transform matrix. This model was built using only
 212 the condition-independent activity by averaging the firing rates for individual spiking units across all
 213 trials regardless of the movement condition (i.e. target location).

214 The condition-independent activity was then submitted to jPCA (Churchland et al., 2012) to
 215 identify the two-dimensional neural plane with the most rotational/cyclic activity. In this model, the
 216 changes in firing rate can grow/shrink along a single dimension (synchronous) as well as rotate across
 217 dimensions (asynchronous). The eigen decomposition of the transform matrix yields eigenvalues with the
 218 real part representing growing or shrinking away from the origin while the imaginary part represents
 219 rotations. Note, this utilization of the jPCA algorithm on only the condition-independent activity is
 220 different than the typical application of jPCA to data containing the condition-dependent activity.
 221 Additionally, we find the results of the dynamical system are more stable when the firing rates are square-
 222 root transformed to equalize variance between high and low firing rates (Kihlberg et al., 1972; Snedecor

223 and Cochran, 1980; Ashe and Georgopoulos, 1994) and thus performed this transform before submitting
 224 firing rates to jPCA.

225 We call the plane with the most rotation the condition-independent (CI) plane and define the two
 226 neural dimensions that define this plane as CIx and CIy. To consistently define CIx and CIy across
 227 recording sessions and monkeys, we defined the +CIx direction as the neural dimension that had the
 228 maximum average firing rate. This was performed by calculating the population averaged firing rate at
 229 all angles in the plane and rotating the CIx and CIy axes so that +CIx aligned with the largest firing rate.
 230 Having identified this jPC neural plane, our work introduces a new analytic variable—condition-
 231 independent phase (CI ϕ)—which estimates the instantaneous phase angle within this two-dimensional
 232 plane of the projected population firing rates. We calculate CI ϕ using the Hilbert transform applied to the
 233 two signals, CIx and CIy, generating a complex, analytical representation of the population signal. The
 234 angle of this complex signal is then used to calculate the instantaneous phase.

235 Since our task consisted of highly variable trial lengths and timing, the identification of
 236 condition-independent activity by time averaging based upon behavioral events was challenging. To be
 237 less constrained in identifying the plane with condition-independent rotational activity, we used an
 238 iterative approach alternating between identifying the CI ϕ for each time point and then averaging the
 239 condition-independent neural activity for each CI ϕ value. We first time-averaged the activity aligned on
 240 speed peaks, and then initially performed jPCA on the time-averaged data. After identifying the rotational
 241 plane, we then binned and averaged the firing rates based on its phase in the plane (rather than time) and
 242 performed jPCA on this new phase-averaged neural activity. This calculation of the jPCA plane and
 243 phase averaging was repeated for three iterations to ensure convergence. The Matlab code and additional
 244 documentation about the calculation of CI ϕ as described in the paper is freely available online at
 245 <https://github.com/arouseKUMC/CIphase>. The code is also available as Extended Data 1.

246 The calculation of the jPC plane and the CI ϕ was performed using 5-fold cross-validation. Each
 247 recording session was divided into 5 testing sets of trials each containing 20% of the data. The jPC plane

248 was calculated by training on the other 80% of the data and then tested on each test set. All presented
 249 results for CI ϕ are using the test data projected into the jPC dimensions identified by the separate training
 250 set.

251 *Firing Rate vs. Speed Model*

252 For comparison with our two-dimensional CI plane and phase analysis, we wanted to examine
 253 how well a linear predictor of speed using a single neural dimension could perform. We therefore
 254 performed linear regression to predict speed from the recorded neural firing rates. For this estimate, we
 255 regressed the firing rates for all recorded units to peak speed for all submovements. We utilized the firing
 256 rates for each recorded unit averaged across a time window from 300 ms before to 100 ms after each peak
 257 speed. We chose this method to identify a neural dimension that correlated with speed without using
 258 separate time lags for each individual neuron. For motor cortex, the neural signal in this dimension would
 259 be expected to increase and peak before each peak in movement speed. We identify and report the time at
 260 which the peaks in this neural signal occurred to quantify how accurately the timing of peaks in
 261 movement speed was predicted.

262 *Statistics*

263 Several statistical analyses (Table 1) were used to assess how similar corrective submovements
 264 were to initial submovements and whether there were repeated cycles of neural activity and if these cycles
 265 corresponded to behavior. For correlations between submovement speed profiles, movement times, and
 266 average spike times, non-parametric tests were used. Since CI ϕ values represent an angle ranging from $-\pi$
 267 to π , circular distribution statistics—mean, variance, correlation, and Rayleigh test for non-uniformity—
 268 were used. All circular statistics were calculated with CircStat, a Circular Statistics Toolbox for Matlab
 269 (Berens, 2009).

270 Table 1. Statistical tests and confidence intervals reported throughout this study referenced with letter
 271 superscripts.

	Data Structure	Type of test	Confidence intervals
a	Correlation between speed profiles from -200 to 200 ms relative to peak speed, nonparametric	Wilcoxon rank sum test	[25 th , 75 th] percentiles
b	Initial vs. Corrective movement times, nonparametric	Two-sided Wilcoxon rank sum test	Percentage of submovements within 100-350 ms
c	Initial vs. Corrective Average spike times between -200 to 100ms, nonparametric	Spearman's rank correlation	95% confidence interval by bootstrapping (1000 repetitions)
d	Circular distribution of phase	Rayleigh test	Circular standard deviation
e	CI ϕ -angle Speed – linear random variable	Circular correlation between angle and linear variable	Minimum and maximum across 12 recording sessions
f	Ratio of Standard deviations of times estimated with CI ϕ and Firing rate model	F-test	95% confidence interval

272

273 **Results**274 *Motor behavior – initial and corrective submovements*

275 Movement speed was analyzed throughout the center-out task from instruction until successful
276 completion of the final target hold. The two monkeys successfully completed 10,963 (monkey P) and
277 8,737 (monkey Q) trials across 12 recording sessions each. In addition to the peaks in speed with the
278 initial reach after instruction, additional peaks in speed were observed and labeled as corrective
279 submovements. There were 6478 and 3912 corrective submovements identified for monkeys P and Q,
280 respectively. Across all trials, 68.3% (P) and 71.1% (Q) were completed in a single initial movement,

281 17.5% (P) and 20.3% (Q) of trials were completed with one additional corrective submovement, and
 282 14.2% (P) and 8.6% (Q) of trials required two or more corrective submovements. The location of the
 283 identified speed peaks within example trials and the speed profiles for monkey P are shown in Figure 2A
 284 and 2B, respectively. The speed peaks tended to be distinct with nearly zero velocity between most
 285 peaks. As shown in Figure 2C, 99.0% (P) and 97.7% (Q) of the minimum speed trough following the
 286 initial speed peak were less than 20% of the peak. Similarly, 82.4% (P) and 85.8% (Q) of the troughs
 287 were less than 20% of the preceding peak between sequential corrective speed peaks. The mean peak
 288 speeds for initial submovements were 1533 (P) and 1182 (Q) pixels/s while corrective submovement peak
 289 speeds were 460 (P) and 400 (Q) pixels/s. Thus, the average peaks for corrective submovements were
 290 30.0% and 33.8% of initial submovements, and a low-speed trough almost always occurred between two
 291 speed peaks making it reasonable to analyze submovements defined by their peak speeds.

292 <Insert Figure 2 near here>

293 The speed profiles were time aligned to peak speed to better examine the identified
 294 submovements (Figure 3A). Almost all submovements show a clear bell-shaped profile for both the
 295 initial and corrective movements. The similarity between initial and corrective speed profiles was
 296 assessed by using the correlation between randomly selected pairs of movements. For random pairs
 297 (irrespective of trial) of one initial and one corrective submovement, the median correlation was 0.78
 298 [0.58 0.89] (monkey P) and 0.83 [0.70, 0.90] (monkey Q). Thus, the shape of corrective submovements
 299 was significantly correlated with the shape of initial submovements ($p < 0.001^a$). As a ceiling comparison,
 300 the correlation between randomly selected pairs of initial submovements was observed to be 0.93 [0.86
 301 0.96] (P) and 0.91 [0.80, 0.96] (Q). Even though the shape of initial-corrective pairs was significantly
 302 less correlated than the initial-initial pairs, corrective submovements still had a similarity measure that
 303 was a large percentage—84% (0.78/0.93) and 91% (0.82/0.91)—of that observed for initial-initial pairs.

304 The time duration and timing of submovements was also examined. The onset and offset of
 305 submovements were defined as the time points when speed was one-half of the maximum speed both

306 before and after the speed peak. As shown in Figure 3B, the movement duration at half maximum speed
 307 was similar and close to symmetric for both initial and corrective submovements. The initial
 308 submovements were slightly longer having a median time of 220ms (P) and 270ms (Q) compared to
 309 corrective submovements with medians of 180ms (P) and 220ms (Q). This difference in median
 310 movement times was statistically significant ($p < 0.001^b$) but the difference of 40 and 50ms was small,
 311 especially given the peak speed was only one-third the magnitude for the smaller corrective movements.
 312 Overall, all submovement durations, as measured by the full width at half maximum, occurred within a
 313 similar range with 96.7%/88.0% (P/Q) of all initial and 96.3%/93.0% (P/Q) corrective submovements
 314 between 100-350 ms. The time between speed peaks—either initial to first corrective submovements or
 315 between subsequent corrective submovements—is plotted in Figure 3C. The median time between peaks
 316 were 570 ms for monkey P and 700 ms for monkey Q with the mode time between peaks being 450ms (P)
 317 and 550ms (Q). Only 3.2% (P) and 0.1% (Q) of speed peaks had a time between peaks less than 200ms
 318 and 6.1% (P) and 10.0% (Q) of speed peak pairs had times greater than 1200 ms. These observations
 319 suggest the movement behavior could be divided into submovements with similar bell-shaped velocity
 320 profiles and similar time durations.

321 <Insert Figure 3 near here>

322

323 *Consistent Timing of Neural Firing Rates for Initial and Corrective Submovements*

324 Single target acquisition movements thus often consisted of initial and corrective submovements
 325 with similar temporal characteristics. Did neural activity in the primary motor cortex control such target-
 326 acquisition movements as a single movement, or as a series of discrete submovements? The neural firing
 327 rates across the recorded population were time aligned to the submovement speed peaks to examine the
 328 firing rates from 500 ms before until 300 ms after the peak speed. The average firing rate (smoothed with
 329 a Gaussian window, $\sigma = 30\text{ms}$) for all analyzed units aligned to the peak speed for initial and corrective
 330 submovements are shown in Figure 4A. A clear peak occurs before the peak speed for both initial and

331 corrective submovements in both monkeys. Monkey P's peak firing rates occurred 170 ms and 120 ms
 332 before initial and corrective submovements, respectively, while monkey Q's occurred at 160 and 160 ms
 333 before for both initial and corrective submovements. Thus, firing rates increased and peaked globally for
 334 corrective submovements in addition to the initial reach.

335 If all neurons had the same time lag preceding the upcoming peak in movement speed, there
 336 would be a synchronized increase and decrease of all condition-independent firing rates simultaneously.
 337 However, when examining average firing rates from 10 example neurons from one recording session
 338 from monkey P, all aligned to peak speed, we see heterogenous timing of firing rates relative to the peak
 339 speed (Figure 4B). This relationship tended to be conserved across initial and corrective movements,
 340 with the purple spiking units tending to fire earlier and the orange units later for both initial and corrective
 341 submovements. This suggests that the condition-independent neural activity across the neurons might
 342 form a repeatable temporal structure—a neural trajectory—that is more than a simple simultaneous rise
 343 and fall in firing rate across the population

344 To quantify the early versus late consistency of spiking units, we calculated the average time of
 345 all spikes that occurred within a window from -200ms before to 100ms after peak speed to determine
 346 whether a unit tended to increase its firing rate earlier (negative time) or later (positive time) relative to
 347 peak speed. We then compared these average spike times for initial versus corrective submovements for
 348 each spiking unit. As shown in Figure 4C, earlier firing units (more negative) for initial submovements
 349 tended to fire earlier for corrective submovements, while units later (more positive) for initial
 350 submovements also tended to fire later for corrective submovements. This correlation was significant for
 351 all spiking units with Spearman correlations of $\rho = 0.40$ [0.35, 0.45] (P) and $\rho = 0.58$ [0.53, 0.62] (Q),
 352 $p < 0.001^c$. Using only single units, the Spearman correlations were $\rho = 0.37$ [0.31, 0.44] (P) and $\rho = 0.61$
 353 [0.54, 0.68] (Q), $p < 0.001^c$. Thus, a significant portion of the ordered timing of units was conserved
 354 relative to peaks in movement speed for both initial and corrective submovements.

355 <Insert Figure 4 near here>

356 *Consistent Neural Dynamics for Initial and Corrective Submovements*

357 We next wanted to examine whether these repeatable neural patterns that occurred on average
 358 across all movements could be used to identify submovements on individual trials. Despite the smaller
 359 magnitude of the condition-independent neural activity during corrective movements, the repeated
 360 oscillations in speed and repeated neural dynamics suggested a portion of neural activity was repeatable
 361 and common to initial and corrective submovements. To examine this, we built a simple linear dynamical
 362 system model using the neural firing rates from the entire trial—including both initial and corrective
 363 submovements—to characterize common temporal dynamics that might be present. The neural firing
 364 rates were again averaged across all conditions, i.e. movement directions, and both initial and corrective
 365 portions of the trials so the dynamical system model would identify common condition-independent
 366 activity. Using the jPCA algorithm described in Churchland et al. (2012), i) the first six principal
 367 components of the neural space and ii) the two dimension plane within the space of those six principal
 368 components that captured the most rotational neural activity were identified. We labeled the two neural
 369 dimensions of the plane with the most rotational condition-independent activity as C_{Ix} and C_{Iy}. To
 370 consistently define C_{Ix} and C_{Iy} across recording sessions and monkeys, we aligned the +C_{Ix} direction
 371 with the neural dimension that had the maximum average firing rate in the plane. This was performed by
 372 calculating the average firing rate across all spiking units for neural activity based on each timepoint's
 373 angle in the C_{Ix}/C_{Iy} plane (binned in 100 angle intervals) and rotating the C_{Ix} and C_{Iy} axes so that +C_{Ix}
 374 aligned with the angle with largest firing rate. This alignment results in the +C_{Ix} dimension closely
 375 aligning with the time course of the global average firing rate across the population (shown in Fig 4A)
 376 while C_{Iy} is an orthogonal neural dimension that oscillates with a phase lag of $\pi/2$ compared to C_{Ix}.

377 The average firing rates projected in our identified CI plane for all initial and corrective
 378 submovements are shown in Figure 5, where the neural data was again aligned relative to peak speed for
 379 initial and corrective submovements separately. The neural trajectory in the 2-dimensional C_{Ix}/C_{Iy} plane
 380 are shown in Figure 5A, while the same C_{Ix} and C_{Iy} dimensions are plotted as a function of time in

Figure 5B. The initial and corrective neural trajectories (Fig. 5A) are very similar in their shape and direction of rotation within the plane, with the trajectories for corrective submovements appearing as an additional cycle resembling a smaller, scaled version of the larger trajectories for initial submovements moving from the -CIy to +CIx to +CIy to -CIx dimensions. The time courses of CIx (solid) and CIy (dashed) (Fig. 5B) were similar for initial (blue) and corrective (red) submovements, though they differed in magnitude. The peak in the CIx dimension (denoted with an X)—defined as the dimension in the plane that best correlated with the global average firing rate of the population—occurred approximately 150 ms before peak speed for initial and corrective submovements, whereas the peak in the CIy dimension (also denoted with an X) occurred near the time of peak speed for both submovement types.

<Insert Figure 5 near here>

Neural cycles improve predictions of behavioral timing

Since the population firing rates in the CI plane appeared to cycle across the two dimensions with similar timing for initial and corrective submovements, despite different magnitudes, we next chose to examine the instantaneous phases of CIx and CIy activity to see if it was a statistically significant marker of the neural state of motor cortex and its relationship with upcoming movement. We used a Hilbert transform to create an analytic representation of the CIx and CIy signals and then calculated the instantaneous phase by taking the angle between the real component and the Hilbert transformed imaginary component. The average phase of CIx and CIy for both initial and corrective submovements—time aligned to peak speed—is shown in Figure 6A. The phase of CIx (solid lines) and that of CIy (dashed lines) each were similar for initial and corrective submovements, with the zero phase of CIx occurring about 150 ms before the peak speed while CIy lagged CIx with an approximately $\pi/2$ phase lag, with the zero crossing occurring around peak speed. The slope of the phase for corrective movements was slightly steeper indicating that neural activity cycled slightly faster for corrective movements than initial. Histograms of the phase of CIx and of CIy at peak speed on individual trials are shown in Figure 6B. The distributions of phases of CIx and CIy were significantly non-uniform for both monkeys and the

means and standard deviations are given in Table 2. Thus, there was a clear relationship between peak speed and the phase of condition-independent activity that occurred with almost all submovements, both initial and corrective, and had similar timing.

<Insert Figure 6 near here>

Table 2. Means and standard deviations of the phase of CIx and CIy. All circular distributions of the phase of CIx and CIy were non-uniform (all $p < 0.001^d$).

Monkey P	CIx Mean	CIx Std. dev	CIy Mean	CIy Std. dev
Initial	0.35π	0.26π	-0.14π	0.23π
Corrective	0.43π	0.33π	-0.15π	0.36π
Monkey Q				
Initial	0.31π	0.22π	-0.15π	0.30π
Corrective	0.45π	0.31π	-0.05π	0.37π

Because the phase in the CI plane appeared to define the neural dynamics and predict upcoming speed peaks, we created a metric we call the condition-independent phase (CI ϕ) by averaging the phase of CIx and phase of CIy + $\pi/2$ to calculate the current phase in the CI plane. We then examined the continuous relationship between cursor speed and neural CI ϕ . In figure 7A, we have plotted the cursor speed as a function of CI ϕ . While the CI ϕ is an angle that ranges between $\pm\pi$ radians when calculated, for purposes of display here we have incremented CI ϕ in steps of 2π to show how successive cycles of neural activity (abscissa) were related to movement speed (ordinate) as individual trials progressed through both initial and subsequent corrective submovements. The individual trials for monkey P in Figure 7A are the same as the trials shown in Figure 2B. However, the speed traces have now been stretched or condensed in time based on the current brain state measured with the CI ϕ . This plot now shows that the speed of movement varied with the cyclic neural activity with the cursor speeds for most

424 trials rising and falling in 2π cycles of $CI\phi$. Both the speed averaged across all trials (white) and the non-
 425 uniform occurrence of peak speeds in individual trials (black) demonstrate that movement speed was
 426 consistently correlated with the cycles of condition-independent neural activity. The statistically
 427 significant circular correlation between speed and $CI\phi$ was 0.44 [0.39,0.53] and 0.42 [0.35,0.50]
 428 ($p < 0.001^e$ for both animals) with the largest speeds occurring at $CI\phi = 0.32\pi$ and $0.31\pi (+2k\pi)$ for
 429 monkeys P and Q, respectively.

430 Finally, we examined the predictive power of $CI\phi$ for estimating when the peak speed occurred.
 431 Figure 7B illustrates the distribution of the time at which $CI\phi = 0$ relative to the time of peak speed for
 432 initial submovements (top) and corrective submovements (bottom). These distributions consistently
 433 peaked 100-150 ms before the speed peak for both initial and corrective submovements. Corrective
 434 movements had $CI\phi = 0$ at times slightly closer to peak speed indicating that the time delay to peak speed
 435 was slightly less for corrective movements. A relatively consistent relationship between neural activity in
 436 the CIx/CIy plane and peak speed was present for both initial and corrective submovements across all
 437 trials regardless of target size or reach direction.

438 To examine if incorporating neural dynamics significantly improved prediction, we compared our
 439 $CI\phi$ predictions with these population dynamics to predictions using a standard approach of using the
 440 instantaneous firing rate of all units to predict peak speeds. For predictions with the instantaneous firing
 441 rates, we built a linear regression model to estimate speed with a weighted sum of the instantaneous firing
 442 rate (a single neural dimension) of all spiking units (see Methods). Using this model, we estimated the
 443 time when the peak in firing rate in the neural dimension occurred that predicted the upcoming speed
 444 peak. Figure 7C shows the temporal distributions of these peak firing rates relative to peak speed for
 445 both initial and corrective submovements. Like the distributions using the dynamical model above
 446 (Figure 7B), the firing rate model peaked 150 to 100 ms before peak speed. The peaks were broader by
 447 10-20 ms, however, as characterized by the greater standard deviations (σ) given for each distribution.
 448 The standard deviations were significantly different in all cases—initial and corrective for both monkeys

(Table 2). Furthermore, although $\geq 84\%$ of submovements were included in each of these distributions (percentages given in Fig. 7), a small fraction of submovements could not be aligned, lacking a $CI\phi=0$ in the dynamical systems model and/or a peak in the firing rate model within the -300 to 100 ms time window examined. The percentage of these unaligned trials was consistently smaller for the dynamical systems model. Compared to using only the instantaneous/synchronous firing rates in a single neural dimension, using the cyclic/asynchronous dynamics of the neural population significantly improved the accuracy and consistency with which the time of peak speed could be predicted.

<Insert Figure 7 near here>

Table 3. Comparison of predication accuracy as measured with standard deviation in predictions using the dynamical system $CI\phi$ model vs. an instantaneous firing rate model.

	σ_1 , CI ϕ , (ms)	σ_2 , Firing Rate (ms)	F-stat, $\frac{\sigma_1^2}{\sigma_2^2}$	95% Confid. interval	Data Comparison	Statistical Test
Initial					All submovements with a prediction between -300:100 ms, assuming normal distribution	F-test ^f , all p<0.001
Monkey P	66.1	84.4	0.61	[0.59, 0.64]		
Monkey Q	75.1	91.1	0.69	[0.65, 0.71]		
Corrective						
Monkey P	88.0	104.2	0.71	[0.68, 0.75]		
Monkey Q	87.0	98.7	2.06	[0.73, 0.83]		

Discussion

Our precision center-out task utilized small targets to elicit one or more corrective submovements in many trials. We found a temporal relationship for both initial and corrective reaching movements with cyclic, condition-independent neural activity. Rather than a single cycle of neural activity in the primary

465 motor cortex occurring during each trial, the speed profiles of initial and corrective submovements each
 466 aligned with a cycle of neural activity, providing a useful neural marker encoding the series of
 467 submovements.

468 In our precision center-out task, the monkeys' movements showed consistent bell-shaped speed
 469 profiles. These speed profiles were evident for both the larger initial movement from the center toward
 470 the peripheral target as well as for each subsequent corrective movement. A large majority of both initial
 471 and corrective submovements had durations of 100-350 ms, with a low-speed trough separating almost all
 472 submovements. Discrete submovements defined by multiple speed peaks have previously been described
 473 in behavioral studies of reaching (Pratt et al., 1994; Lee et al., 1997; Hatsopoulos et al., 2007; Polyakov et
 474 al., 2009), turning a knob (Novak et al., 2000), isometric contractions (Massey et al., 1992; Hall et al.,
 475 2014), and object manipulation for tactile discrimination (Pruszynski et al., 2018). The experimental
 476 results and analysis presented here provide new evidence of a relationship between condition-independent
 477 neural dynamics and such behaviorally observed submovements.

478 *Condition-independent phase predictive of cursor speed*

479 Churchland et al. (2012) originally described a single cycle of condition-dependent rotational
 480 dynamics in the activity of neurons in the primary motor and premotor cortex during both straight reaches
 481 and curved reaches around obstacles. More recently, Zimnik and Churchland (2021) demonstrated two
 482 repeated cycles of neural activity, each shortened in time, when a pair of movements were simultaneously
 483 instructed to be performed in rapid succession. Here, by focusing on the shifting dimensions of
 484 condition-independent neural activity with time, we identified that cycles of neural activity appear not
 485 only for initially planned reaches but also for the highly variable, corrective submovements that are made
 486 online with visual feedback. Our results highlight that the various time lags between individual cortical
 487 neurons' firing and the upcoming reaching movements are conserved, whether large and instructed or
 488 small and made online with feedback.

489 *Similar but smaller cyclic, condition-independent activity for corrective movements*

490 Although the orientation and direction of rotation through the identified condition-independent
 491 neural dimensions was similar for initial and corrective submovements, the magnitude of the condition-
 492 independent neural activity that occurred for corrective submovements was approximately one-third to
 493 one-half the magnitude of that for the initial submovements (both in average firing rate, Fig. 4A, and
 494 within our identified rotational CI plane, Fig. 5). On average, the encoding of movement speed is clearly
 495 present in primary motor cortex (Moran and Schwartz, 1999; Paninski et al., 2004), and the smaller
 496 change in average firing rate observed here during corrective movements reflected the lower movement
 497 speed for the corrective compared to the initial submovements, suggesting speed tuning in the magnitude
 498 of the condition-independent activity. This does not imply, however, that each individual trial and each
 499 individual neuron have proportionally smaller changes of firing rate during smaller amplitude
 500 movements. Examination of small, instructed movements has shown that a fraction of primary motor
 501 cortex neurons have similar firing rates for small, precise and for larger wrist movements while others are
 502 selective for only larger movements (Fromm and Evarts, 1981). We too observed similar large changes in
 503 firing rate on individual corrective submovements for certain neurons (data not shown). Only when
 504 averaging firing rates—time aligned to the peak movement speed or the decoded condition-independent
 505 phase—were the population differences in firing rate modulation between initial and corrective
 506 movements readily apparent. Precisely identifying encoded speed on a trial-by-trial basis with the neural
 507 activity remains challenging as there are often large changes of firing rates for individual neurons that are
 508 variable and idiosyncratic during any particular corrective submovement.

509 Our results highlight that condition-independent neural signals can evolve in time along with the
 510 neural dynamics that are related to task conditions. Adding condition-independent activity to condition-
 511 dependent activity has been suggested to make brain dynamics more robust to noise by increasing the
 512 differences in neural signals even when the muscle activation pattern at certain time points are very
 513 similar (Russo et al., 2018). In the context of precise, corrective movements, we speculate cyclic brain

514 dynamics can be used to organize neural activity that creates distinct submovements with time-varying
 515 neural and musculoskeletal dynamics that are more reliable for motor control. Previous reports of neural
 516 activity defining submovements linked together have used the term movement fragments (Hatsopoulos et
 517 al., 2007). In the context of precise movements, we hypothesize that organizing movement into
 518 submovements or movement fragments might allow the control of particular submovements to have
 519 different encoding features, neural processing, or control policies, for instance, allowing the large initial
 520 movements to be larger amplitude and less precise while the corrective submovements are smaller and
 521 more precise. Further studies will be needed to understand the condition-dependent differences that
 522 accompany the condition-independent neural features presented here.

523 Though various time lags in different neurons seem likely to be present across many tasks, cyclic,
 524 condition-independent neural dynamics may not be similar for all upper extremity movements. For
 525 instance, whereas during combined reach-and-grasp movements cyclic condition-independent activity
 526 occurs along with more complex condition-dependent dynamics (Rouse and Schieber, 2018), during
 527 separate reaching movements and grasping movements condition-dependent activity was cyclic during
 528 reaching, but was more complex during grasping (Suresh et al., 2020). The neural signals in a given
 529 hemisphere for cyclic movements of the contra- and ipsilateral arms have also have been reported to be in
 530 orthogonal subspaces (Ames and Churchland, 2019). Cyclic neural activity may not be due only to
 531 intrinsic neural dynamics in M1, but also the result of sensorimotor feedback control and/or a cognitive
 532 strategy. With sufficient time delay between each submovement, the neural activity could fit both
 533 descriptions. Observations of additional submovements defined by second or third speed peaks do not
 534 necessarily require a feedback controller with discrete updates. A single, continuous optimal feedback
 535 controller with appropriate delays and signal dependent noise can generate additional submovements with
 536 multiple, sequential speed peaks (Li et al., 2018). Results by Susilaradeya et al. (2019) argue that
 537 extrinsic effects of a task interact with the intrinsic dynamics of the brain in a manner consistent with an
 538 optimal feedback controller, possibly providing a framework for assessing these effects across a variety of

539 tasks including our precision center-out task. Further work examining neural activity in various tasks
 540 and/or additional sensorimotor brain areas will be needed to advance our understanding of the neural
 541 dynamics of the sensory processing, cognitive planning, and motor execution for precise, corrective
 542 movements.

543 The cyclic dynamics of corrective movements have important implications for brain-computer
 544 interfaces (BCIs). To date, most BCI decoders are time-invariant, not recognizing when submovements
 545 occur. Decoders are typically first constructed from observed or imagined movements that assume single,
 546 straight-line movements. When algorithms for updating BCI decoders consider the change in movement
 547 direction for corrective movements, it typically has been assumed the intended path is updated
 548 continuously (Gilja et al., 2012; Shanechi et al., 2016). Experiments have suggested that BCI control can
 549 be improved with two states: active control and rest (Kim et al., 2011; Williams et al., 2013, 2016; Sachs
 550 et al., 2016). Our results suggest that computing the phase of cyclic, condition-independent neural
 551 activity with $CI\phi$ (Fig. 7B) can provide better prediction of the timing of corrective submovements than
 552 using the instantaneous firing rates alone (Fig. 7C). This may lead to BCIs that allow the subject to better
 553 signal when they intend to make a corrective movement. With additional information about the typical
 554 neural dynamics and kinematics of submovements, BCI decoders may better estimate natural kinematics
 555 from noisy neural signals. Taking into account the cyclic dynamics of the condition-independent neural
 556 activity may also lead to better descriptions of the condition-dependent activity that encodes task features.
 557 For example, direction encoding has been shown to shift progressively during a single movement (Sergio
 558 and Kalaska, 1998; Churchland and Shenoy, 2007; Suminski et al., 2015; Suway et al., 2017). Accounting
 559 for the phase of a movement with its cyclic, condition-independent activity (i.e. $CI\phi$) could enable
 560 decoders of movement direction that shift progressive during a single movement. Such improvements
 561 could lead to a more robust description of the neural encoding of precise and corrective movements.

562

563

564 Figure 1. Idealized representation of both the synchronous and rotational components of condition-
 565 independent and -dependent changes in neuronal firing rate. A) The firing rates for four neurons (blue,
 566 orange, yellow, and purple) are shown for reaches to four target directions (light to dark grayscale). The
 567 overall firing rates differ for both the four neurons and the four target condition. By time averaging
 568 across the four conditions, the condition-independent firing rates and the residual condition-dependent
 569 firing rates are both identified. B) Next, averaging across the population reveals that firing rates are i)
 570 synchronous activity across all neurons at each time point and ii) the remaining, asynchronous/rotational
 571 firing rate changes specific for each neuron. C) The neural space visualizes the population activity by
 572 showing each neuron's firing rate as a point along an orthogonal dimension with time represented as a
 573 trajectory through this space. In this representation, the difference between synchronous and rotational
 574 activity is better appreciated. Synchronous activity is movement along a single neural dimension while
 575 rotational activity is movement between dimensions. Note, the dimensions defined by individual neurons
 576 are shown projected in a 2D plane. Only the given component (synchronous/rotational and condition-
 577 independent/-dependent) are shown for these four example neurons for visualization purposes. In a much
 578 higher dimensional space when recording from a large number of neurons, the possibility of finding
 579 dimensions with little overlap between components is much greater.

580

581 Figure 2. The precision center-out task. A) Cursor paths for four example trials to each target for the
 582 three target sizes: regular (top), narrow (middle), shallow (bottom). Initial submovements from 200ms
 583 before to 200ms after speed peaks are plotted in blue with the point when peak speed occurred shown
 584 with a blue dot. Corrective movements are similarly identified in red with a red dot. Grey lines connect
 585 the rest of a trial before, between, or after submovements with a speed peak. B) Cursor speed plotted
 586 versus time for a subset of trials. Initial (blue) and corrective (red) submovement speed peaks are
 587 identified with squares. Gray squares identify speed peaks that were thrown out because they i) were
 588 small initial movements that did not move outside the center or ii) occurred entirely within the peripheral

589 target. C) Top) Distribution of peak speeds for initial (blue) and corrective (red) submovements. Bottom)
 590 Distribution of the trough-to-peak ratio for the troughs following an initial submovement before a
 591 corrective submovements and following a corrective submovement before another corrective
 592 submovement. Data is shown for monkey P. Data for monkey Q, which had similar results, is not shown.

593

594 Figure 3. Time course of submovements. A) The cursor speeds are plotted aligned to speed peaks for
 595 initial (blue) and corrective (red) submovements. N.B. The cursor speeds shown are before the bandpass
 596 filter used for identifying peaks displayed in Figure 1B. Thus, the maximum of each trace may not align
 597 exactly with the plotted peak speed. B) Histogram of the time at half-maximum speed before and after
 598 peak speed for all initial (blue) and corrective (red) submovements. C) The time duration between speed
 599 peaks including the times from initial submovement to first corrective submovement as well as between
 600 any consecutive pairs of corrective submovements.

601

602 Figure 4. Neural firing relative to initial and corrective submovements. A) The firing rate for all spiking
 603 units was averaged for all initial (blue) and corrective (red) submovements. The shaded region interval
 604 shows the 95% confidence interval of the calculated mean for all spiking units. Circles indicate the time
 605 of peak firing rate for each condition. B) Average condition-independent firing rates for 10 example
 606 spiking units recorded simultaneously from monkey P time-aligned relative to peak speed for all initial
 607 (left) and corrective (right) submovements. Firing rates are shown relative to the average firing rate
 608 within the given time window (initial or corrective) for each spiking unit. The weighted timing of spikes
 609 (in ms) within the -200ms to 100ms window is given for each unit. Units are colored based on the initial
 610 movement by whether their firing rates were greater early (purple) or late (orange). C) Weighted timing
 611 of spiking relative to peak speed for each unit for initial (abscissa) and corrective (ordinate)
 612 submovements. More negative times represent spiking earlier relative to the peak speed of each

submovement. Single units are shown with filled circles while all other spiking multi-units are shown with open circles.

Figure 5. Cyclic neural dynamics related to initial and corrective submovements. A) The average population firing rates for initial (blue) and corrective (red) submovements are projected in the CIx/CIy plane identified with jPCA. The trajectories start at the triangles and end at the squares. Each filled circle is a 150 ms time step and the open corresponds to peak speed. C). Average CIx (solid lines) and CIy (dashed lines) plotted as a function of time relative to average cursor speed (dotted lines).

Figure 6. Phase of CIx and CIy relative to peak cursor speed. A) Phase of CIx (solid lines) and CIy (dashed lines) time-aligned to peak speed (Time = 0) and averaged for all initial (blue) and corrective (red) submovements. B) Histograms of the phase of CIx and CIy at the time of peak speed for initial (blue) and corrective (red) submovements. Means and standard deviations are given in Table 2.

Figure 7. Relationship between CI ϕ and cursor speed. A) Cursor speed is plotted as a function of CI ϕ for 200 trials with at least one corrective submovement. The average speed of all trials as a function of CI ϕ is shown in white, illustrating the oscillation in cursor speed depending on the phase of neural activity. The circular correlations between CI ϕ and cursor speed for all corrective trials were 0.44 [0.39, 0.53] and 0.43 [0.36, 0.50] for monkeys P and Q, respectively, $p < 0.001^e$ in both cases. Note, the unwrapped CI ϕ is not always a monotonically increasing value as occasionally the neural activity could reverse and move clockwise rather than counter-clockwise in the neural plane shown in Figure 6B.

B & C) Identifying the times of peak speeds with a dynamical systems model (B) or with an instantaneous firing rates (C). The time point when CI $\phi = 0$ (B) or peak firing rate (C) was used as a prediction of the upcoming submovement. Each histogram shows only those submovements for which the neural data aligned with the movement data, i.e. CI $\phi = 0$ (B) or maximum firing rate (C) occurred within the time range examined (-300 to 100 ms relative to submovement peak speed). The percentage of

638 total aligned trials is shown for each distribution as well as the standard deviation (σ) for the aligned
639 trials. In all cases, the dynamical systems model predictions were more precise, with a narrower standard
640 deviation (statistics in Table 3) and fewer unaligned trials.
641

642

643 Extended Data 1. Matlab code to calculate the CI ϕ is available on Github.

644

645 Since the trial data contains corrective movements in addition to the large initial movements that
646 were not precisely time aligned to trial events for averaging condition-independent neural activity, we
647 developed a novel algorithm to iteratively average the firing rates, calculate CI ϕ , then average the firing
648 rates again based on the CI ϕ . This iterative process involves three steps: i) Each unit's firing rate is
649 averaged across all trials to determine its condition-independent firing rate. ii) Dimensionality reduction
650 is performed using PCA and jPCA on the condition-independent firing rates to identify the neural plane
651 with the most rotational/cyclic condition-independent activity. iii) The instantaneous phase is calculated
652 using the Hilbert transform on the first two jPC dimensions for all data points. Matlab code is available
653 on GitHub. Further details are available in the Readme document attached to the code.

653

654

655

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