Most theories of motor cortex have assumed that neural activity represents movement parameters. This view derives from what is known about primary visual cortex, where neural activity represents patterns of light. Yet it is unclear how well the analogy between motor and visual cortex holds. Single-neuron responses in motor cortex are complex, and there is marked disagreement regarding which movement parameters are represented. A better analogy might be with other motor systems, where a common principle is rhythmic neural activity. Here we find that motor cortex responses during reaching contain a brief but strong oscillatory component, something quite unexpected for a non–periodic behaviour. Oscillation amplitude and phase followed naturally from the preparatory state, suggesting a mechanistic role for preparatory neural activity. These results demonstrate an unexpected yet surprisingly simple structure in the population response. This underlying structure explains many of the confusing features of individual neural responses.

Motor and premotor cortex were among the first cortical areas to be extensively studied1. Yet their basic response properties are poorly understood, and it remains controversial whether neural activity relates to muscles or to abstract movement features2–13. At the heart of this debate is the complexity of individual neural responses, which exhibit a great variety of multiphasic patterns4,14,15. One explanation is that responses represent many movement parameters:

\[ r_n(t) = f_n(param_1(t), param_2(t), param_3(t), \ldots) \]

where \( r_n(t) \) is the firing rate of neuron \( n \) at time \( t \), \( f_n \) is a tuning function, and \( param_1(t), param_2(t), \ldots \) are arguments such as hand velocity or target position. Alternatively, motor cortex may constitute a dynamical system that generates and controls movement4,8,14–17. In its simplest, deterministic form this can be expressed as:

\[ \dot{r}(t) = f(r(t)) + u(t) \]

where \( r \) is a vector describing the firing rate of all neurons (the ‘population response’ or ‘neural state’), \( f \) is its derivative, \( f \) is an unknown function, and \( u \) is an external input. In this conception, neural responses reflect underlying dynamics and display ‘tuning’ only incidentally18,19. If so, then dynamical features should be present in the population response. In looking for dynamical structure, we focused on a common principle for movement generation across the animal kingdom: the production of rhythmic, oscillatory activity20–22.

Rhythmic responses in different systems

We first examined neural responses in a context where rhythmic pattern generation is known to occur. The medicinal leech generates rhythmic muscle contractions at \( \sim 1.5 \text{ Hz} \) during swimming23, and many single neurons display firing rate oscillations at that frequency (Fig. 1a)24,25. Rhythmic structure was also present for cortical responses in the walking monkey: \( \sim 1 \text{ Hz} \) oscillations matching the \( \sim 1 \text{ Hz} \) movement of the arm (Fig. 1b). If single-neuron oscillations are generated by population-level dynamics, then the population response (the neural state) should rotate with time26, much as the state of a pendulum rotates in the space defined by velocity and position. We projected the population response onto a two-dimensional state space and found rotations of the neural state for both the swimming leech (Fig. 1d; projection of 164 simultaneously recorded neurons) and the walking monkey (Fig. 1e; projection of 32 simultaneously recorded neurons; also see Supplementary Movie 1). These observations, although not trivial, are largely expected for a neural dynamical system that generates rhythmic output22.

The projections in Fig. 1d, e were obtained via two steps. The first was the application of principal component analysis (PCA) to the population response. Inconveniently, PCA does not find dimensions relevant to dynamical structure. We therefore used a novel method that finds an informative plane within the top principal components (PCs). To be conservative, this ‘JPCA’ method was applied only to the top six PCs, which contain the six response patterns most strongly present in the data. The mathematical underpinnings regarding JPCA are described below, but the following is critical. Application of JPCA results in six PCs: an orthonormal basis that spans exactly the same space as the first six PCs (Supplementary Movie 2). The first two PCs capture the strongest rotational tendency in the data. The JPC projections are simply linear projections of response patterns that are strongly present in the data; if a given pattern is not present in the top six PCs it cannot be present in the JPCs.

The central finding of this study is that quasi-oscillatory neural responses are present during reaches. This is illustrated by the average firing rate of an example motor cortex neuron (Fig. 1c) and the corresponding population-level projection (Fig. 1f). The rotation of the neural state is short lived (\( \sim 1 \text{ cycle} \)) but otherwise resembles rotations seen during rhythmic movement. This finding is surprising—the reaches themselves are not rhythmic—yet it agrees with recent theoretical suggestions20,22. There might be a concern that the patterns in
**Figure 1** | Oscillation of neural firing rates during three movement types.

*Fig. 1c, f are idiosyncratic. But, as shown below, rotations of the neural state are one of the most prominent features of the data.*

**Quasi-rhythmic responses during reaching**

We analysed 469 single-neuron recordings from motor and premotor cortex of four monkeys (identified as A, B, J, N). We made a further 364 simultaneous recordings (single and multi-unit isolations) from two pairs of implanted 96-electrode arrays (monkeys J, N). Monkeys executed straight reaches (monkeys A, B) or straight and curved reaches (monkeys J, N). An instructed delay paradigm allowed monkeys to prepare their reaches before a go cue. We analysed 9 data sets, each using 27–108 reach types (‘conditions’). For each neuron and condition we computed and analysed the average across-trial firing rate. Most neurons exhibited preparatory and movement-related responses (Fig. 2). Responses were typically complex, multiphasic and heterogeneous. Yet there appear to be oscillations in many single-neuron responses, beginning just before movement onset and lasting for ~1–1.5 cycles. These quasi-oscillatory patterns were seen for all reach types and all monkeys. Yet interpretational caution is warranted: multiphasic responses might exist for any number of reasons. The critical question is whether there exists orderly rotational structure, across conditions, at the population level.

We have proposed that motor cortex responses reflect the evolution of a neural dynamical system, starting at an initial state set by preparatory activity. If the rotations of the neural state (Fig. 1f) reflect straightforward dynamics, then similar rotations should be seen for all conditions. In particular, the neural state should rotate in the same direction for all conditions, even when reaches are in opposition.

We projected the population response for all conditions onto the jPC plane. This was done for 200 ms of data, beginning when preparatory activity transitions to movement-related activity (Supplementary Movie 3 shows a longer span of time). The resulting projections (Fig. 3a–f) show four notable features. First, rotations of the neural state are one of the most prominent features of the data.
the neural state are prevalent during reaching. Second, the neural state rotates in the same direction across conditions (Fig. 3, different traces). Third, the rotation phase follows naturally from the preparatory state. Last, state-space rotations do not relate directly to reach curvature. Monkeys A and B executed straight reaches; monkeys J and N executed a mixture of straight reaches, clockwise-curving reaches, and anticlockwise-curving reaches (Fig. 2, insets). Yet for each data set the neural state rotates in the same direction across conditions. Rotations appear to reflect dynamics that are consistent across conditions, rather than the pattern of kinematics per se.

If the initial population-level preparatory state is known (Fig. 3, circles) subsequent states are reasonably predictable. Such predictability is absent at the individual-neuron level: the correlation between preparatory- and movement-tuning activities parallels approximately zero. Nevertheless, the ordered state-space rotations relate directly to the seemingly disordered single-neuron responses. Each axis of the jPCA projection captures a time-varying pattern that resembles a single-neuron response (Supplementary Fig. 1). Single neurons strongly reflect combinations of these underlying patterns. However, that underlying structure is not readily apparent when plotting each pattern alone, or each neuron individually. Furthermore, the rotations during reaching are quasi-oscillatory, lasting only 1–1.5 cycles (Fig. 1c; also see Supplementary Movie 3). Their brevity and high frequency (up to ∼2.5 Hz) makes them easy to miss unless trial counts are high (data sets averaged 810 trials per neuron) and data are precisely aligned on movement onset (Methods).

**Rotations, kinematics and EMG**

Traditional views posit that motor cortex neurons are tuned for movement parameters such as direction. This perspective does not naturally account for the data in Fig. 3. We simulated neural populations that were directionally tuned for velocity with an additional non-directional sensitivity to speed. Simulated preparatory activity was tuned for reach direction and distance. We simulated one ‘velocity model’ data set per recorded data set, based upon the recorded velocities and endpoints. Firing rates, trial counts, neuron counts and spiking noise were matched to the recorded data. For velocity-model populations, jPCA found no robust or consistent rotations (Fig. 4a, d, h). This was true for all data sets (summary analysis below) including those with curved reaches (for example, Fig. 4h). We also simulated a `complex-kinematic’ model in which responses reflected the weighted sum of kinematic parameters (position, velocity, acceleration and jerk) that correlate with muscle activity. This model produced multiphasic responses but not consistent rotations (Fig. 4b, e, i). We also recorded EMG (electromyograms) from a population of muscles (6–12 recordings per data set). Although EMG is strongly multiphasic, the population of muscles did not show consistent rotations (Fig. 4c, f, j; summary data below). This was not due to the smaller size of the muscle population (Supplementary Fig. 6). In sum, rotations in state space require more than multiphasic responses: they require a pair of orthogonal rotations in state space. The neural network possesses two orthogonal rotations in state space: one at a high frequency and one at a low frequency. Muscle activity was fit as the sum of the resulting oscillations in the temporal domain. For example, when fitting the deltoid EMG for dataset J3 (the third data set from monkey J) the higher-frequency rotation in the model occurred at 2.8 Hz (Fig. 5a). Different conditions (9 and 25 are shown) involved different amplitudes and phases, set by the preparatory state of the model. The vertical, ‘lagging’ dimension drove simulated muscle activity, and the projections onto that dimension (Fig. 5b, c, dark blue) provided key features of the EMG fit. The slower features are provided by a 0.3 Hz oscillation (not shown).

This ‘generator model’ provided excellent EMG fits (Fig. 5b, c and Supplementary Figs 7 and 8). The fit/EMG correlation ranged from...
0.97–0.99 across data sets. Thus, deltoid activity could always be generated from the sum of two underlying rotations whose phases and amplitudes (but not frequencies) vary across conditions. This raises a subtle but key point: although EMG responses do not themselves exhibit state-space rotations, EMG can nevertheless be constructed from underlying rotations. This observation need not imply that cortex directly controls muscles. Yet it illustrates the plausibility of direct control\(^6\), and demonstrates that rotations provide a natural basis for generating non-rhythmic movement.

Faster reaches might have been expected to involve faster rotations, or longer reaches to involve longer rotations. However, EMG could be fit using two rotations with fixed frequency and duration. This was true even though the 27 conditions differed greatly in reach speed and amplitude. One state dimension (‘leading’, on the x-axis) is always 90° ahead of the other (‘lagging’, on the y-axis).

Population-level quantification

To quantify rotation strength we measured the angle from the neural state in the jPCA plane (\(x\)) to its derivative (\(\dot{x}\)) for every condition and time (Fig. 6a). The first jPCA plane is oriented such that the average state in that plane (\(x_{\text{ave}}\)) is at zero (Fig. 6a). The fit to the EMG is the sum of lagging components from the 2.8 Hz rotation (shown) and a lower frequency rotation (0.3 Hz, not shown). These projections onto the leading and lagging dimensions (light and dark blue) versus time (condition 9). The fit to the EMG is the sum of lagging components from the 2.8 Hz rotation (shown) and a lower frequency rotation (0.3 Hz, not shown). c. Similar to b, but for condition 25. The 2.8 Hz rotation is \(\sim 180°\) out of phase with that in b, d. Simulated response of a unit from the generator model (Methods).

Presentation as in Fig. 2. e, a second simulated unit. f, jPCA projection of the simulated population; compare with the neural data in Fig. 3c. g, Hand velocities for the 27 conditions in d, e, f. Red traces show conditions 9 and 25. Successfully reveal the simple underlying rotations (Fig. 5f). These rotations resemble those observed for the neural data (Fig. 3).

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matrix $M$ provides the best performance of any matrix (skew-symmetric matrices are a subset of unconstrained matrices). For the neural data and generator model, the fit provided by $M_{\text{skew}}$ was nearly as good as the fit provided by the best unconstrained $M$ (Fig. 6b). For the velocity-tuned and complex-kinematic models, $M_{\text{skew}}$ performed poorly. Results were similar whether we considered all six dimensions or just the plane with the strongest rotations (the plane defined by the first two jPCs). Thus, of those dynamics that can be captured linearly, rotational dynamics dominate only for the generator model and neural data.

EMG data showed weak rotations (Fig. 6a, b, red), underscoring a central point: state-space rotations result not from a multiphasic signal, but from how that signal is constructed. For example, the generator model exhibits rotations even though the EMG does not. More generally, many features of the observed rotations make sense in terms of how outputs (EMG, kinematics) might be generated, rather than in terms of the outputs themselves. For example, a strong intuition, and a prediction of most hypotheses of motor cortex, is that neural responses should unfold faster for faster movements. However, the generator model makes the opposite prediction; rotation frequencies are fixed. We tested this prediction using two data sets where target colour instructed fast versus slow reaches. Both the generator model and the neural data exhibited rotations that were of similar angular velocity for fast and slow reaches (Fig. 6c, d). The same point can be made by separately applying jPCA for fast and slow reaches: the largest eigenvalues of $M_{\text{skew}}$ were actually slightly smaller for fast reaches (8.8 versus 9.8 radians s$^{-1}$ for monkey A, 12.2 versus 13.5 radians s$^{-1}$ for monkey B). Rotation amplitude, rather than frequency, differed between speeds (Fig. 6c, d). This finding is readily interpretable in light of the generator model: larger-amplitude rotations produce more strongly multiphasic responses, a feature of the EMG necessary to drive larger accelerations/decelerations (also see Supplementary Fig. 9).

**Discussion**

Rotations of the population state are a prominent feature of the cortical response during reaching. Rotations follow naturally from the preparatory state and are consistent in direction and angular velocity across the different reaches that each monkey performed. The rotational structure is much stronger and more consistent than expected from chance or previous models. These population-level rotations are a relatively simple dynamical feature yet explain seemingly complex features of individual-neuron responses, including frequent reversals of preferred direction$^{14,30}$, and the lack of correlation between preparatory and movement-period tuning$^{15,29}$ (Fig. 5d, e and Supplementary Fig. 8). State-space rotations produce briefly oscillatory temporal patterns that provide an effective basis for producing multiphasic muscle activity, suggesting that non-periodic movements may be generated via neural mechanisms resembling those that generate rhythmic movement$^{20,21,31–33}$.

Recent results suggest that preparatory activity sets the initial state of a dynamical system, whose subsequent evolution produces movement activity$^{15}$. Aspects of these dynamics—a rotation away from the preparatory state—appear straightforward. However, the circuitry that creates these dynamics is unclear; it may be purely local, or may involve recurrent circuitry$^{34}$ that links motor cortex with the spinal cord and with subcortical structures$^{35}$. Peripheral feedback is also expected to shape neural dynamics$^{36}$, although this cannot account for the first $\sim 150$ ms of ‘neural motion’ (the hand has yet to move). The finding that dynamics are captured by a skew-symmetric matrix suggests functionally antisymmetric connectivity: a given neural dimension (for example, jPC$_1$) positively influences another (for example, jPC$_2$), which negatively influences the first. However, it is unclear whether this population-level pattern directly reflects a circuit-level dominance of antisymmetric connectivity. We also stress that although rotations are a dominant pattern in the data across multiple dimensions (Supplementary Fig. 4), non-rotational components exist as well, perhaps reflecting the nonlinear dynamics necessary for initiating or terminating movement, for stability$^{37}$, and for feedback control$^{16,38}$.

It is hoped that a focus on the dynamics that generate movement will help transcend the controversy over what single neurons in motor cortex ‘code’ or ‘represent.’ Many of the neural response features that seem most baffling from a representational perspective are natural and straightforward from a population-level dynamical systems perspective. It therefore seems increasing likely that motor cortex can be understood in relatively straightforward terms: as an engine of movement that uses lawful dynamics.
METHODS SUMMARY

Optical recordings from the isolated leech central nervous system were made by K. Briggman and W. Kristan and have been described previously24,25. We recorded neural activity from trained monkeys using both single- and multielectrode techniques. We recorded from the arm representation of premotor cortex using a wireless system while the monkey walked to obtain juice from the front of a treadmill. We recorded from the arm representation of motor and premotor cortex while monkeys reached to targets projected onto a vertically oriented screen, also for a juice reward. All surgical and animal care procedures were performed in accordance with National Institutes of Health guidelines and were approved by the Stanford University Institutional Animal Care and Use Committee.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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METHODS

Recordings and task design. Recordings from the isolated leech central nervous system were made by K. Brigman and W. Kristan and have been described previously.22,23. Recordings from monkey cortex were made using both a delayed reach task (with head restraint) and from an unrestrained monkey walking on a treadmill41. Animal protocols were approved by the Stanford University Institutional Animal Care and Use Committee.

Most analyses concerned data collected during delayed reach tasks, for which our basic methods have been described previously.22,23–25. Briefly, four male rhesus monkeys (A, B, J, and N) performed delayed reaches on a fronto-parallel screen. Delays ranged from 0–1,000 ms (the exact range varied by monkey). Only trials with delays >400 ms were analysed. Fixation was enforced (at the central spot) during the delay for monkeys J and N. We used two variants of a centre-out reaching task. In the ‘speed task’ monkeys A and B reached to radically arranged targets at two distances. Reach speed was instructed by target colour (28 total delays during the delay for monkeys J and N. We used two variants of a centre-out with delays

reach task (with head restraint) and from an unrestrained monkey walking on a treadmill39–41. Animal protocols were approved by the Stanford University

channels were wirelessly transmitted using the HermesD system39,41. Behavioural

treadmill39–41. Animal protocols were approved by the Stanford University

the arm representation of PMd. The times of threshold crossings on 32 of the 96

Supplementary Fig. 5 shows the central analysis divided by area. Seven of the nine data sets (monkey A, B, J1, J2, J3, J4 and N) were recorded with conventional single-electrode techniques. These data sets involved a total of 469 single-unit isolations. The other two data sets (monkey J-array and N-array data sets, 108 conditions were presented in the same recording session. Recordings from three of the four monkeys (A, B and J) have been analysed in prior publications (for example, ref. 15).

Recordings were made from primary motor cortex (M1, both surface and sulcal) and from the adjacent (caudal) aspect of dorsal premotor cortex (PMd). Supplementary Fig. 5 shows the central analysis divided by area. Seven of the nine data sets (monkey A, B, J1, J2, J3, J4 and N) were recorded with conventional single-electrode techniques. These data sets involved a total of 469 single-unit isolations. The other two data sets (monkey J-array, recorded 18 September 2009; monkey N-array, recorded 23 September 2010) used pairs of chronically implanted 96-electrode arrays (Blackrock Microsystems). These array-based data sets involved, respectively, 146 and 218 isolations (each a mix of single and multi-unit isolations).

Arrays were implanted after directly visualizing sulcal landmarks. Single-electrode recordings were guided by stereotaxic criteria, the known response properties of M1 and PMd, and the effects of microstimulation. For all monkeys, at some point the dura was reflected and the sulcal landmarks directly visualized. Recordings were medial to the arcuate spur and lateral to the precentral dimple. Recordings were not made within rostral PMd, near the arcuate sulcus. Sulcal M1, surface M1, and caudal PMd are contiguous. Although there are important differences in their average response properties (for example, delay period activity is more common in PMd), these differences are far from absolute: M1-like neurons are frequently found in caudal PMd and vice versa. Most analyses thus considered all neurons without attempting to divide them on the basis of either anatomy or response properties (although see Supplementary Fig. 5).

For the freely walking monkey, data were recorded from an array implanted in the arm representation of PMd. The times of threshold crossings on 32 of the 96 channels were wirelessly transmitted using the HermesD system41. Behavioural data were recorded using a commercially available video camera. Juice was dispensed at one end of the treadmill, providing incentive for the monkey to walk continuously.

EMG data were collected as described previously22. EMG records were rectified, smoothed and averaged before further analysis. A total of 61 recordings were made from six muscle groups: deltoid, biceps brachii, triceps brachii, trapezius, latissimus dorsi and pectoralis. Most data sets contained multiple recordings from each muscle (for examples, see from each of the three heads of the deltoid). The total number of EMG recordings for some data sets was thus as high as 12. EMG was recorded for all data sets except those recorded using arrays.

Computing average firing rate as a function of time. Average trial counts were high (an average of 810 trials per neuron). To ensure response features were not lost to averaging, a concerted effort was made to compute the average firing rate only over trials with nearly identical reach trajectories. This was done by training to a high level of stereotyped behaviour, and by discarding the few trials for which behaviour was not tightly stereotyped. Average firing rates were further de-noised by filtering with a Gaussian (20 or 24 ms depending on the data set) and using a custom-developed smoothing method that discards idiosyncratic features that are both small and not shared across conditions (see supplementary figure 4 in ref. 15). This method improves the signal-to-noise ratio without over-smoothing in the temporal domain, which was important for preserving high-frequency features of the response. This step aids the visualization of single-neuron firing rates, but had essentially no effect on any of the population-level analyses (Supplementary Fig. 10). EMG recordings and ‘recordings’ of simulated neurons were processed using all the same steps as for the neural data.

Because the delay period and reaction time were variable, firing rates were computed separately locked to target onset, the go cue, and movement onset. For presentation (where one wishes to follow a trace through different epochs) we interpolated over the gaps between the three epochs.

Fitting the generator model to EMG. For the generator model, we directly simulated two state-space rotations. The goal was to start not by simulating the responses of individual units, but by directly simulating the underlying structure of the population data in state space. The two simulated rotations produced patterns that were summed to fit the EMG for the deltid. For example, the deltid EMG for data set J3 was fit using a 2.8 Hz rotation and a 0.3 Hz rotation. Each rotation consisted of leading and lagging sinusoids windowed by a gamma function, with the initial state extended backwards in time to mimic preparatory activity (for example, Fig. 5a, b, c). The amplitude and phase of that rotation was different for every condition, to allow the model to fit the different EMG patterns recorded for each condition. Importantly, for a given data set the rotation always had the same frequency regardless of condition, with a rise and decay defined by the same windowing gamma function (for example, the 2.8 Hz rotation was always at 2.8 Hz and the 0.3 Hz rotation was always at 0.3 Hz). This mimics a dynamical system that is the same across conditions except for an initial state that determines phase and amplitude. EMG was fit as the sum of the lagging sinusoids, one for each of the two frequencies.

Optimization involved two levels. At the level of each individual condition, the amplitudes and phases that provided the best fit were found via regression. Regression exploited the fact that every possible amplitude/phase of a sinusoid can be constructed via a linear combination of a sine and cosine. This step is thus both fast and guaranteed to find the best fit. Regression involved an offset term, which could be different for each condition. At the level of the whole data set, we numerically optimized the two frequencies, the mean and shape parameter of the windowing gamma function, and the time when oscillations began. Optimization was started from many initial parameter choices and the best fit was chosen.

Each condition’s simulated EMG is simply the sum of two windowed sinusoids and a variable offset. However, the central idea of the generator model is that those sinusoids result from rotations in an internal state space. The generator model thus embodied five basic patterns: the pair of leading and lagging template patterns that make up each rotation plus the offset.

Simulated neural data. We produced two classes of simulated neural data sets. The first class (the velocity model and complex-kinematic model) was based on a traditional framework in which units were cosine tuned for EMG-like factors. The second class was based on the generator model described above, which emulates a simple dynamical system. For both classes of model, the firing rates of individual units were assumed to depend upon underlying factors. For the velocity-tuned model, movement-period activity was based upon three underlying factors: horizontal reach velocity, vertical reach velocity, and reach speed (for example, see ref. 27). Each unit thus had a preferred direction in velocity space. Preparatory activity was based upon three additional underlying factors: horizontal reach endpoint, vertical reach endpoint, and peak reach speed. For the complex-kinematic model, we assumed that both movement and muscle activity reflects a variety of kinematic factors (position, velocity, acceleration, jerk) neural activity might share this property41. As with the velocity model, each unit was cosine tuned with a preferred direction in physical space. Simulated activity depended on motion in that preferred direction with the following sensitivities: 25 (spikes s−2 m−1), 10 (spikes s−2 m−1 s−1), 1 (spikes s−2 m−2), 0.05 (spikes s−2 m−3). These constants are taken from a published model2, but have been adjusted as follows. First, the sensitivity to position has been reduced by half, otherwise it tended to dominate to an unrealistic degree. Second, a sensitivity to jerk has been added. This makes for a more stringent control (it increases the multiphasic aspects of the simulated responses) and captures the expectation that cortical activity might be more phasic than muscle activity. Preparatory activity was sensitive to target endpoint.

For the generator model, the underlying factors were the oscillatory patterns captured by the underlying state space. These patterns defined both the movement period and (via the initial state for each pattern) preparatory activity. Also included as underlying factors were the two gamma functions that defined the oscillation envelopes. These factors were the same across all conditions, and were included to mimic the overall change in excitability that is presumed to cause the waxing and waning of oscillations. The inclusion of these un-tuned factors served to increase the variety and realism of the simulated responses, it has essentially no impact on the main analyses (Figs 5g and 6). Those analyses are sensitive only to response aspects that differ among conditions.
The firing rate of each simulated unit was a random combination of the underlying factors. For the velocity and complex-kinematic models, the random combinations resulted in a roughly uniform range of preferred directions for both the preparatory and movement periods. For the generator model, the random combinations resulted in simulated units that typically reflected both oscillation frequencies, with a roughly uniform distribution of phases. This is indeed the default expectation for a large network that supports two oscillatory modes.

To produce simulated data with realistic levels of noise, we ‘recorded’ simulated spikes that were produced via a gamma-interval process (order 2) based on the underlying firing rate. For each neural data set, we simulated one unit for every recorded neuron, and matched the overall firing rates and trial counts of each simulated unit to those of the respective recorded neuron. The simulated spiking data was then analysed just as for the actual neural data. The velocity and complex-kinematic models each produced nine simulated data sets (one for every real data set). The generator model produced seven: it could not be simulated for the J-array or N-array data sets, as we did not attempt to record EMG for those 108-condition experiments.

**Projections that capture rotational structure.** We produced projections of the population data using a novel dimensionality reduction method, jPCA, designed for the present application. For most analyses we analysed 200 ms of time, sampled every 10 ms, starting just before the rapid change in neural activity that precedes movement onset. Before applying jPCA, a number of pre-processing steps were applied to the data (these same steps were also applied to the simulated data and EMG). Responses were normalized to have a similar firing-rate range for all neurons. ‘Soft’ normalization was used, so that neurons with very strong responses were reduced to approximately unity range, but neurons with weak responses had less than unity range. For each neuron, the data were mean-centred at every time: the average across-condition response was subtracted from the response for each condition. Thus, all subsequent analysis focused on those aspects of the neural response that differ across conditions. This pre-processing step can be skipped (see Supplementary Fig. 11) but the resulting projections often capture rotations that are similar for all conditions. In such cases one fails to gain multiple views of the underlying process, making it difficult to infer whether rotations are due to dynamics or to more trivial possibilities. It was thus deemed more conservative to only interpret projections where activity unfolds differently across conditions. Related population analyses (for example, the population vector) achieve the same end implicitly: non-directional aspects of the response cancel out. The pre-processing steps (and all subsequent analysis steps) were applied in the same way to all data sets, real and simulated.

The most critical pre-processing step was the use of traditional PCA. We compiled a data matrix, \( X \), of size \( n \times ct \), where \( n \) is the number of neurons, \( c \) is the number of conditions, and \( t \) is the number of time points. This matrix simply contains the firing rates of every neuron for every condition and every analysed time. We then used PCA to reduce the dimensionality of \( X \) from \( n \times ct \) to \( k \times ct \), \( k = 6 \) for all analyses in the main text, which is conservative given the true dimensionality of the data\(^4\). The resulting \( 6 \times ct \) matrix, \( X_{\text{red}} \), defines a six-dimensional neural state for every time and condition. By pre-processing with PCA, we ensure that when jPCA is subsequently applied, it reveals only patterns of activity that are strongly present across neurons. Pre-processing with PCA greatly reduces any potential concern that the observed rotations were found simply by looking in a very high-dimensional space (also see shuffle controls in Supplementary Figs 2 and 3).

jPCA is a method for finding projections (onto an orthonormal basis) that captures rotational structure in the data. jPCA is based on a comparison of the neural state with its derivative. We computed \( \dot{X}_{\text{red}} \), of size \( 6 \times ct(t - 1) \) by taking the difference in the state between adjacent time points within each row of \( X_{\text{red}} \). We then fit using

\[
\dot{X}_{\text{red}} = MX_{\text{red}}
\]  

and

\[
X_{\text{red}} = M_{\text{skew}}X_{\text{red}}
\]

(To keep the dimensions appropriate, the final time point for each condition in \( X_{\text{red}} \) was removed so that it was also \( 6 \times ct(t - 1) \)). Thus, we are attempting to find matrices \( M \) and \( M_{\text{skew}} \) that take the state at each time in \( X_{\text{red}} \) and transform it into the derivative of the state in \( X_{\text{red}} \). \( M \) can be found using linear regression. Finding \( M_{\text{skew}} \) requires more complex (but still linear) operations (see Supplementary Derivation for more detail). The quality of the above fits was assessed using \( R^2 \) (for example, Fig. 6b). \( R^2 \) captures the ability to linearly predict the data in \( \dot{X}_{\text{red}} \) (across all times and conditions) from the data in \( X_{\text{red}} \). \( M_{\text{skew}} \) has imaginary eigenvalues, and thus captures rotational dynamics. The strongest, most rapid rotations in the dynamical system occur in the plane defined by the eigenvectors associated with the largest two (complex-conjugate) imaginary eigenvalues. These eigenvectors (\( V_1 \) and \( V_2 \)) are complex, but the associated real plane can be found by: \( j\text{PC}_1 = V_1 + V_2 \), and \( j\text{PC}_2 = j(V_1 - V_2) \) (after resolving the ambiguity in the polarity of \( V_1 \) and \( V_2 \) such that their real components have the same sign). The first jPCA projection is then \( X_{\text{jPCA}} = (j\text{PC}_1; j\text{PC}_2) \times X_{\text{red}} \). The matrix \( X_{\text{jPCA}} \) is thus of size \( 2 \times ct \), and describes the neural state, projected onto two dimensions, for every time and condition. For a given PCA plane, the choice of orthogonal vectors (jPC\(_1\) and jPC\(_2\)) within that plane is arbitrary. We therefore selected jPC\(_1\) and jPC\(_2\) so that any net rotation was anticlockwise (the same choice was of course used across all conditions for a given data set) and so that the spread of preparatory states was strongest along jPC\(_1\). We also computed the proportion of the total data variance captured by the jPCA plane, in a manner exactly analogous to that for PCA.

It is worth stressing that the six jPCs form an orthonormal basis that spans exactly the same space as the first six PCs. Thus, all patterns seen in the jPCA projections are also present in the PCA projections (the rotational patterns are simply not axis aligned in the latter case, and are thus less obvious to the eye; see Supplementary Movie 2).

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