

Simplified and effective motor control based on muscle synergies to exploit musculoskeletal dynamics

Max Berniker^a, Anthony Jarc^b, Emilio Bizzi^{c,1}, and Matthew C. Tresch^{a,b,d,2}

^aDepartment of Physical Medicine and Rehabilitation, Northwestern University and Rehabilitation Institute of Chicago, 345 East Superior Street ONT-931, Chicago, IL 60611; ^bDepartment of Biomedical Engineering, Northwestern University, 2145 Sheridan Road, Evanston, IL 60208; ^cDepartment of Brain and Cognitive Sciences and McGovern Institute for Brain Research, Massachusetts Institute of Technology, Building 46-3160, Cambridge, MA 02139; and ^dDepartment of Physiology, Feinberg School of Medicine, Northwestern University, Ward 5-281, Physiology, 303 East Chicago Avenue, Chicago, IL 60611

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The basic hypothesis of producing a range of behaviors using a small set of motor commands has been proposed in various forms to explain motor behaviors ranging from basic reflexes to complex voluntary movements. Yet many fundamental questions regarding this long-standing hypothesis remain unanswered. Indeed, given the prominent nonlinearities and high dimensionality inherent in the control of biological limbs, the basic feasibility of a low-dimensional controller and an underlying principle for its creation has remained elusive. We propose a principle for the design of such a controller, that it endeavors to control the natural dynamics of the limb, taking into account the nature of the task being performed. Using this principle, we obtained a low-dimensional model of the hindlimb and a set of muscle synergies to command it. We demonstrate that this set of synergies was capable of producing effective control, establishing the viability of this muscle synergy hypothesis. Finally, by combining the low-dimensional model and the muscle synergies we were able to build a relatively simple controller whose overall performance was close to that of the system's full-dimensional nonlinear controller. Taken together, the results of this study establish that a low-dimensional controller is capable of simplifying control without degrading performance.

low-dimensional | optimal control | muscle pattern | frog | computational model

Controlling any movement, whether it be a stereotyped reflex or a sophisticated skill, is highly complex. Fundamentally, every movement requires the detailed specification of a vast number of variables, potentially involving many thousands of motor units distributed throughout the limbs and body. Further, the relationship between these variables and the intended motion of the body is nontrivial, dictated by the intricate nonlinear dynamics of the musculoskeletal system. Elucidating control strategies that can overcome these complexities is a central issue in the neural control of movement.

Many investigators have suggested that the central nervous system (CNS) might have developed strategies to simplify the control of movement (1–6). According to one common proposal, the CNS might produce movement through the flexible combination of “muscle synergies,” with each such synergy specifying a particular balance of activation across a set of muscles (7–16). By reducing the number of controlled variables, such a low-dimensional control strategy would simplify the production of movement.

Although many experiments have found evidence to suggest that many behaviors can be produced through combinations of muscle synergies, several questions concerning this hypothesis remain unresolved. Foremost among these questions is a proof of the concept's viability: can a low-dimensional control scheme based on muscle synergies reproduce the range of observed behaviors with negligible loss of efficacy? Given the nonlinearities and high dimensionality inherent in biological motor control, the answer to this question is not obvious. Yet, until this question is answered in the affirmative, the finding that the structure of muscle electrographic data appears to be shared by a small number of

recurring muscle patterns remains only an enticing observation of ambiguous functional significance.

In this study, we evaluate the efficacy of using this approach to control a biologically realistic model of the frog hindlimb. Using techniques from control theory, we examine a method for designing a low-dimensional controller that balances the advantages of exploiting a system's natural dynamics with the need to accurately represent the variables relevant for control. The resulting low-dimensional controller provides an approximation to the natural dynamics and a set of muscle synergies best suited for controlling it. We show that this low-dimensional controller and its attendant muscle synergies are in fact capable of producing movements without a substantial loss of either efficacy or efficiency; i.e., the intended movements are achieved successfully and with minimal effort. Further, we show that not any set of synergies allows for such effective control: this efficacy results when synergies are chosen to exploit the dynamic properties of the limb, meaning that they exploit the movements that the limb produces naturally. Finally, we present evidence suggesting that the muscle synergies we derive may indeed resemble muscle synergies that occur in nature. These results therefore provide direct support for the viability of the muscle synergy hypothesis, suggesting that the CNS might use such a strategy to produce movement simply and effectively.

Results

Overview. We first created a low-dimensional dynamical model that captured the natural dynamics of the frog hindlimb. The examples of “passive walkers” that locomote with negligible active control clearly suggest the utility of such a design principle (17, 18). This work suggests that some limb movements arise “naturally,” and with little muscular effort. Using a technique of nonlinear system balancing we found such a low-dimensional model and then used this model to identify a set of muscle synergies. By design, these muscle synergies control the limb's natural dynamics that are most relevant for a given task. We next analyzed the structure of the identified muscle synergies and their correspondence with experimentally derived muscle synergies. We performed the same analyses with a set of muscle synergies specified according to an alternative hypothesis, that muscle synergies span the range of joint torques. We then used techniques of optimal control to find the activations of these synergies necessary to produce a range of movements. The movements and commands produced using these muscle synergies were compared with those produced when each muscle could be activated independently or when the alternate set

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¹To whom correspondence may be addressed. E-mail: ebizzi@mit.edu.

²To whom correspondence may be addressed at: Northwestern University, Ward 5-281, Physiology, 303 East Chicago Avenue, Chicago, IL 60611. E-mail: m-tresch@northwestern.edu.

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of muscle synergies was used. Finally, we combined the low-dimensional model and muscle synergies to construct a relatively simple controller and evaluated the performance of this controller relative to the full-dimensional nonlinear controller.

Musculoskeletal System. All analyses are based on a physiologically realistic description of the frog hindlimb, *Rana pipiens* (see refs. 19 and 20 for details), consisting of the masses and inertias of the hindlimb skeleton and 13 muscles. The model is a 17-dimensional nonlinear dynamical system, composed of the activation state of the 13 muscles along with the hip and knee joint angles and velocities, as summarized in the system's state equations: $dx/dt = f(x, u)$; $y = Cx$, where x is the system's state (17-dimensional), u is the motor command (13-dimensional), and y is the system's output (a 4-dimensional vector of the joint angles and velocities). Model details can be found in the [supporting information \(SI\) Text](#) and ref. 21.

Identifying Low-Dimensional Natural Dynamics of the Hindlimb. Model-order reduction aims to create simplified descriptions of dynamical systems. Balanced truncation is one such reduction procedure, with the goal of identifying a low-dimensional representation of a system's input–output dynamics* (22, 38). System balancing is based on two properties of dynamical systems. The first property characterizes how control inputs affect system states and is summarized by the controllability gramian. The second property characterizes how system states affect outputs, summarized by the observability gramian [grammians are related to but differ from controllability and observability matrices (23)]. These two grammians are mathematical descriptions of the amount of energy in the state variables excited by control inputs (controllability) and the amount of energy in system outputs excited by the state variables (observability). Taken together, these properties characterize the input–output dynamics, summarizing how commands influence system outputs. For nonlinear systems, such as the musculoskeletal system analyzed here, these grammians can be estimated empirically by exciting control inputs and system states and observing the resulting system dynamics (see [SI Text](#) and ref. 22).

We used these two grammians to identify a balanced state representation, $x' = Tx$, where T is the transformation to a balanced state variable, x' . By using both controllability and observability grammians in this transformation, the procedure “balances” these two basic aspects of the system dynamics. In this balanced representation, the elements of the state variable are ranked by their importance in transforming inputs into outputs. The matrix T can then be truncated, resulting in a k -dimensional state variable, $z = T_k x$. This low-dimensional state, z , is therefore the representation that most succinctly captures the limb dynamics relevant for control.

We then estimated the dynamics of the low-dimensional state, z . We applied pulse commands to each muscle and simulated the resulting limb trajectories. These trajectories were transformed into the low-dimensional state variable z and then fit to a dynamical model of the frog hindlimb: $dz/dt = A_k z + B_k u$; $\hat{y} = C_k z$. Limb trajectories generated by activating each muscle were compared with estimates produced with the low-dimensional model. The similarity between these two sets of trajectories was quantified by the square of the correlation coefficient to obtain the amount of explained variance (or centered R^2). If this model is useful for specifying control, it should estimate the consequences of motor commands accurately (i.e., it should be an accurate forward model). We found that across these output trajectories a 5-dimensional model predicted the actual trajectories very well ($R^2 = 0.99$, rms error of 0.02 rad and 0.12 rad/s). As shown in a later section

*Newman JA, Krishnaprasad PS, Computing balanced realizations for nonlinear systems. Proceedings of the 14th International Symposium on Mathematical Theory of Networks and Systems, June 19–23, 2000, Perpignan, France.

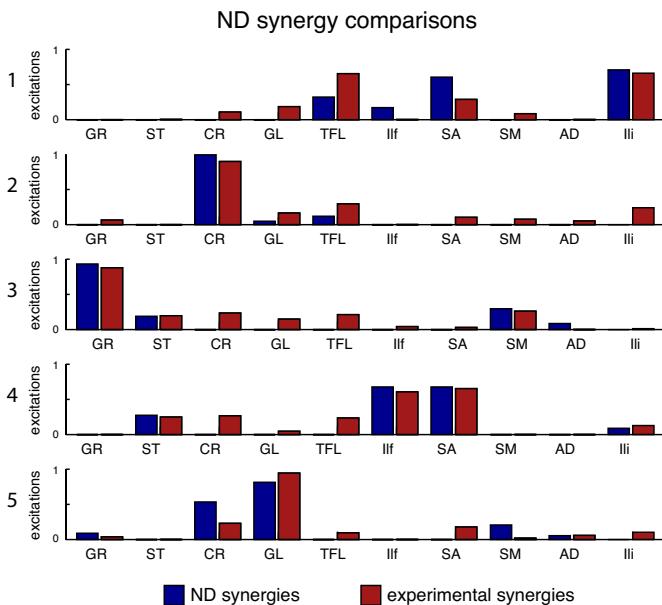


Fig. 1. Muscle synergies identified for the control of natural limb dynamics and their closest experimental matches. Only those 10 muscles that were both recorded experimentally and included in the hindlimb model are shown. The activation strength for each muscle within a synergy is indicated by the bar height. Each bar in a synergy is normalized by the vector norm of the synergy. Blue bars are synergies identified by the system-balancing procedures described in the text. Red bars are the best-matching experimental synergies. The 10 muscles are gracilis (GR), semitendinosus (ST), curarlis (CR), gluteus (GL), tensor facia latae (TFL), iliofibularis (IIf), sartorius (SA), semimembranosus (SM), adductor (AD), and iliocaudalis (Ili).

(*Assessment of Controller Dimensionality*), a low-dimensional controller using 5 synergies performed substantially better than one with 4 synergies and was only marginally worse than a controller with 6 dimensions. We therefore present the results obtained by using a 5-dimensional representation.

Identifying Muscle Synergies for Controlling the Limb's Natural Dynamics. The above analyses result in a low-dimensional model of the frog hindlimb that captures the dynamics most relevant for controlling a particular task variable. In this model, the matrix B_k characterizes how control variables u (muscle excitations) affect the low-dimensional state variable z . B_k therefore defines combinations of muscle excitations that are most important in exciting the natural limb dynamics. Because B_k has a null space, only a small number of such muscle combinations will affect the low-dimensional dynamics; any motor commands in the null space will only minimally excite the natural limb dynamics. A low-dimensional controller therefore utilizes a lower, k -dimensional control signal, which consists of combinations of the original high-dimensional control inputs. These combinations correspond to a set of muscle synergies that, by design, will be those that best excite the natural dynamics of the limb (referred to as ND synergies). The choice of these muscle synergies is further constrained: because muscles cannot push, the muscle synergies should allow for only nonnegative motor commands. The set of ND synergies was found by using an iterative optimization based on these criteria (see *Methods*).

The identified ND synergies are shown in Fig. 1. In general, these synergies had a focused action on a particular joint of the limb. For instance, synergy 3 consists mainly of gracilis (GR) and semimembranosus (SM), which are both hip extensors. Similar muscle combinations can be seen for the other synergies, suggesting that the system-balancing techniques created a biomechanically reasonable decomposition of the hindlimb musculature. Note, however,

that this decomposition was not obvious a priori because most muscles in the hindlimb span multiple joints, making it difficult to classify the action of each muscle. Thus, the principle proposed here was capable of identifying a set of muscle synergies that were sensibly, but not trivially, related to the biomechanical properties of the limb.

We compared these ND synergies with muscle synergies found experimentally across jumping and swimming behaviors in intact frogs (24). Synergies were combined across behaviors and animals to create a large set of experimentally observed synergies (45 synergies observed across 4 frogs). Inner products between ND synergies and experimental synergies were computed to quantify similarity. An inner product of 0 or 1 indicated two dissimilar synergies or two identical synergies, respectively. In Fig. 1, the most similar experimental synergy is presented for each of the ND synergies, showing a high similarity between the two sets of synergies. To interpret the magnitude of this similarity, we compared it with the distribution of similarities expected by chance (see *SI Text*), expressing the observed similarity in terms of the standard normal variable, Z . Thus, if Z was 1.0, it would indicate a similarity that was 1 standard deviation from the expected value. For each of the comparisons shown in Fig. 1, the Z value was >2 (corresponding to $P < 0.025$). However, because of the large number of comparisons made here (with 45 experimental synergies), these values were not significant after a Bonferroni correction.

To evaluate these results further, we performed the same analyses with a set of muscle synergies specified according to an alternative hypothesis. These alternate synergies were designed to span the range of joint torques (referred to as JT synergies). Under this hypothesis, the motivation for a set of muscle synergies is to ensure that joint torques can be produced in all directions (see *Methods*). Such a hypothesis is related to the “feasible force sets” raised in considerations of muscle actions (25, 26). For each JT synergy, we found the most similar experimental synergy (see Fig. S1) and calculated the standard normal variable Z . We then assessed whether the ND synergies were more similar to experimental synergies than were these JT synergies. The average Z values for the ND best-matched synergies were significantly larger than those of the JT best matches (2.3 ± 0.2 and 1.8 ± 0.4 , respectively, $P < 0.05$). These results suggest that the principle proposed here for specifying muscle synergies in terms of the limb’s natural dynamics might be similar to the coordination strategies used by the CNS to specify the synergies underlying natural behaviors.

Evaluating Low-Dimensional Control Based on Muscle Synergies. The primary goal of this study was to evaluate our hypothesis that a low-dimensional controller based on exploiting natural dynamics would allow for simple but effective motor control. The muscle synergies identified in the previous section should be well suited to this goal. Therefore, our first step was the evaluation of these synergies for control. We examined the movements produced using a controller based on ND muscle synergies and compared them with movements produced by alternate controllers (Fig. 2). For each controller, we found the commands (either muscle activations or synergy weights) necessary to produce movement to a target while minimizing a specified cost (see *Methods*).

For the first controller, we assumed that each muscle could be activated independently and that the full-dimensional state was known (controller 1 in Fig. 2). The movements produced by this controller represented the best possible performance of the system, in that all potential control signals could be used. In the second controller, the ND muscle synergies were used to control the hindlimb (controller 2 in Fig. 2). This is the simplest version of a low-dimensional controller: it has accurate, full-dimensional state information but only affects the limb through low-dimensional muscle synergies. If this controller is effective, its performance should be similar to that of the best-case controller.

We found that the performance of the two controllers was very

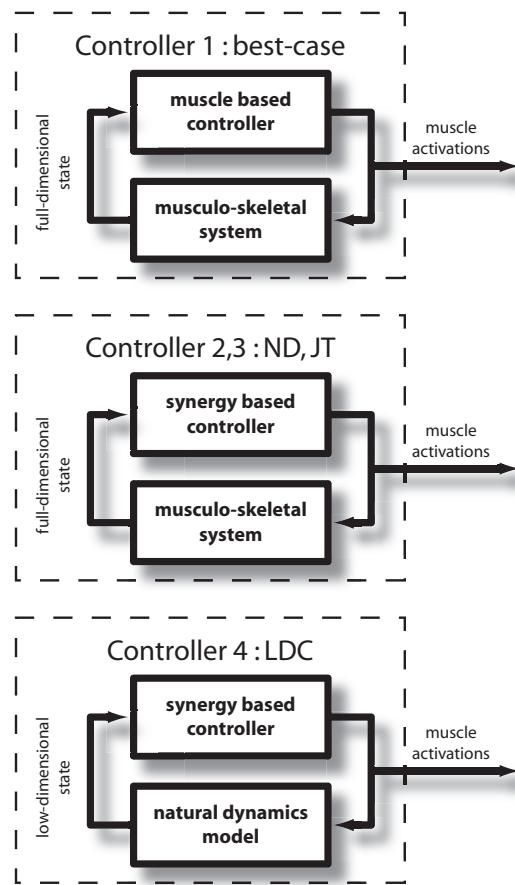


Fig. 2. Illustration of the different controller designs considered. (Top) Full-dimensional controller with access to the full state of the system, which can activate each muscle independently (best-case controller). (Middle) Controller with access to the full state but that activates muscles through synergies. (Bottom) Low-dimensional controller (LDC) with access to a low-dimensional state variable and that uses muscle synergies, thereby simplifying control even further.

similar. Fig. 3*A* shows the trajectories produced by the controller using ND synergies and those produced by the best-case controller. As can be seen qualitatively, the trajectories produced by the controller using ND synergies were very similar to those of the best-case controller. We quantified this similarity by the amount of explained variance between the best-case controller’s trajectories and the ND controller’s trajectories. As can be seen (Fig. 4*A*), the ND synergies performance was very similar to that of the best-case controller. We also evaluated this similarity by calculating the rms error between the trajectories produced by each controller. The rms errors between the two controllers’ trajectories (joint angles and joint velocities) averaged across the six movements were $6.8 \times 10^{-3} \pm 2.3 \times 10^{-3}$ rad and $2.9 \times 10^{-2} \pm 1.0 \times 10^{-3}$ rad/s. The commands produced by using the ND synergies were also very similar to those produced by using the best-case controller (see Figs. 3*B* and 4*B*; the average rms error was $2.1 \times 10^{-3} \pm 1.8 \times 10^{-3}$). This similarity demonstrates that the control strategy using only the ND synergies results in performance that is close to the best that the system can perform. These results also demonstrate that a simplified low-dimensional controller, using only 5 command variables (of the 13 possible), allowed for effective motor control with little degradation from optimal performance.

We then evaluated whether the efficacy demonstrated with the controller based on ND synergies would be observed with a controller based on an alternate set of synergies. This alternate

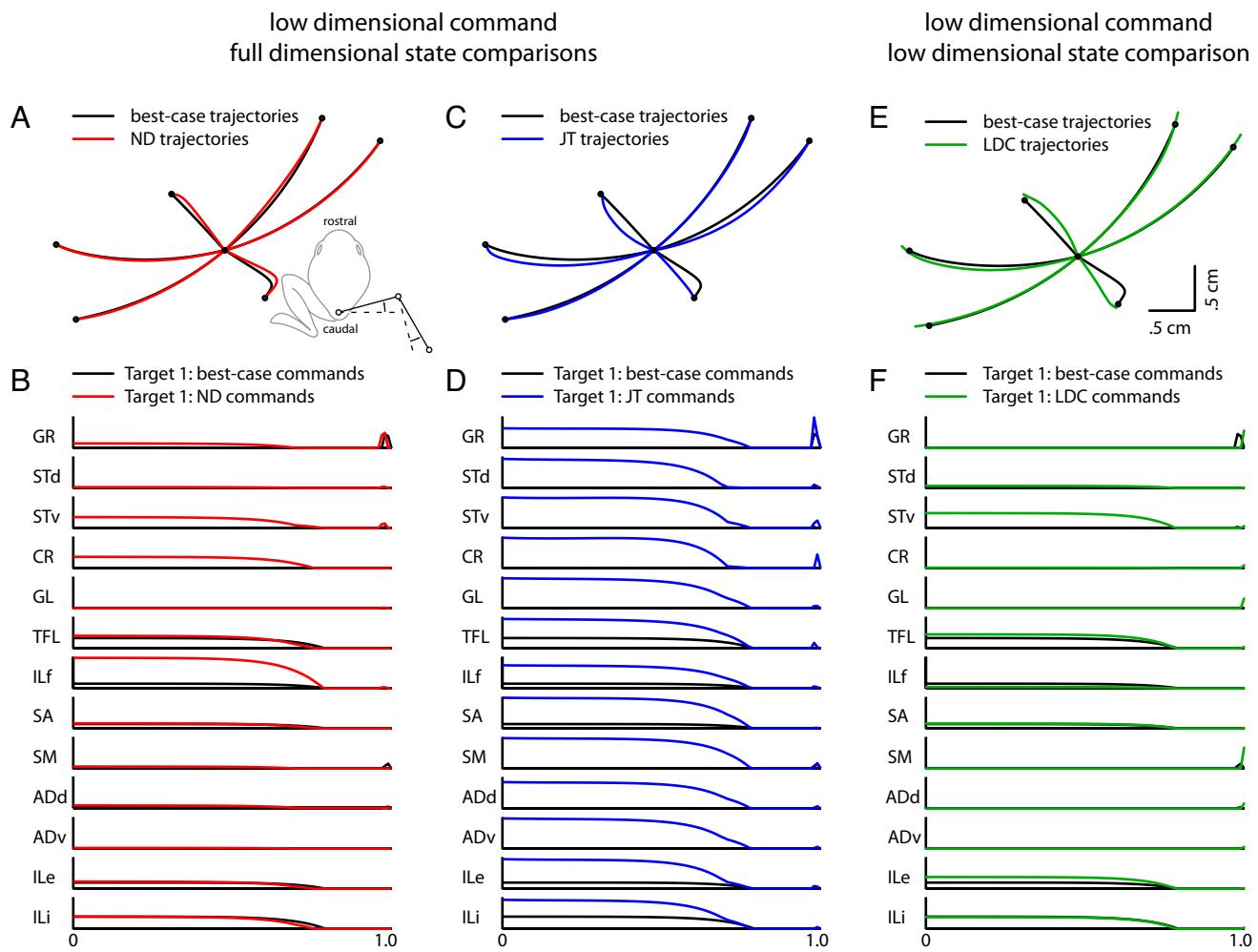


Fig. 3. Performance of the four controllers. For comparison, the optimal limb trajectories and commands (for the movement to target 1, the topmost target) for the best-case controller are displayed in each panel (black traces). (A) Optimal limb trajectories for the ND (red) controller (best-case trajectories in black). (Inset) Hindlimb orientation. (B) Thirteen muscle commands for the ND (red) controller and best-case controller (black). (C) Optimal limb trajectories for the JT (blue) controller. (D) Thirteen muscle commands for the JT (blue) controller. (E) Optimal limb trajectories for the low-dimensional controller (LDC) (green). (F) Thirteen muscle commands for the low-dimensional controller (green).

controller had the same restricted controller dimension as the second controller but was based on JT synergies (controller 3 in Fig. 2). If the principle proposed here for choosing muscle synergies is a good design principle for low-dimensional control, the ND synergies should perform better than this alternate set of synergies.

The trajectories produced by using the JT synergy-based con-

troller are displayed in Fig. 3C. In general, these trajectories were qualitatively similar to those of the best-case and ND controllers. However, there was a small decrease in performance, as seen in a few trajectories (e.g., the up-left and down-right movements in Fig. 3C). As shown in Fig. 4A, this difference was significant, with the trajectories produced by the JT controller being less similar to the best-case controller than those produced by the ND controller ($P < 0.005$). The degraded performance of the JT controller was even greater when comparing controller commands. These commands are shown in Fig. 3D, indicating clearly that the JT controller commands were very different from those of the best-case controller. The variance explained in the commands using the JT synergies was lower ($P < 0.005$) than that explained by the ND synergies (see Fig. 4B). The averaged rms errors between the best-case and JT trajectories were $1.8 \times 10^{-2} \pm 8.8 \times 10^{-3}$ rad and $7.5 \times 10^{-2} \pm 3.6 \times 10^{-2}$ rad/s, whereas the averaged rms error in commands was $2.2 \times 10^{-2} \pm 1.5 \times 10^{-2}$. Comparing these numbers with those of the ND controller further demonstrates a degraded performance. Thus, not any set of muscle synergies allows for effective control: the synergies designed according to the principle proposed here are especially effective.

The above controllers differ only in how they command the musculature, either activating individual muscles (best-case con-

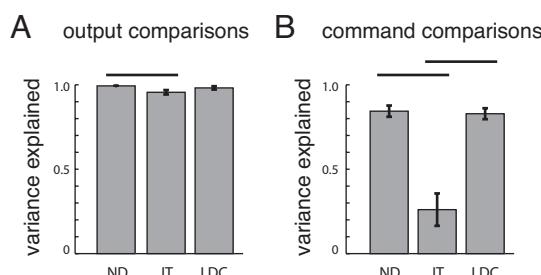


Fig. 4. Comparison of the performance of controllers in relation to the best-case controller. The amount of explained variance (centered R^2) was used to calculate the similarity of the trajectories (A) and commands (B) for each controller to those of the best-case controller. Values are averaged across the six trajectories. Horizontal bars indicate values that are significantly distinct.

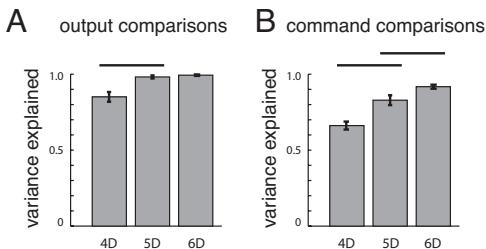


Fig. 5. Assessment of controller dimensionality. The similarity to the best-case controller trajectories (A) and commands (B) of those produced by the low-dimensional controller when its dimension was varied between 4 and 6 is shown. Note that these low-dimensional controllers correspond to controller 4 of Fig. 1, in which both state and control variables are low-dimensional. Horizontal bars indicate values that are significantly distinct.

troller) or activating muscle synergies (controllers using ND and JT synergies). Each controller, however, acts with knowledge of the full-dimensional state of the hindlimb. Controlling this high-dimensional state still presents significant computational difficulties. We therefore evaluated the efficacy of a fourth controller that used the ND muscle synergies in combination with the low-dimensional model of the hindlimb's natural dynamics, rather than the full-dimensional hindlimb state (controller 4 in Fig. 2). The resulting low-dimensional controller is both low-dimensional in state and command, removing the full-dimensional nonlinear system from the control loop and greatly simplifying the control problem. We compared the performance of this controller with that of the best-case controller and the two synergy controllers (ND and JT) described above. Fig. 3E shows that the trajectories produced by this final low-dimensional controller were qualitatively similar to those produced by the best-case controller. Furthermore, the variance explained in the best-case trajectories with this controller was not different from the ND case ($P > 0.05$, Fig. 4A). The averaged rms errors from the best-case results were $2.1 \times 10^{-2} \pm 2.9 \times 10^{-3}$ rad and $5.2 \times 10^{-2} \pm 1.9 \times 10^{-2}$ rad/s. However, inspection of these trajectories indicates small discrepancies. These discrepancies are not unexpected because the controller only has access to the approximate limb state. Small approximation errors will accumulate over time, leading to increased discrepancies by the end of the movement. However, commands produced by this controller were very similar to those produced by the best-case controller (see Fig. 4B), in contrast to the commands produced by the JT controller. The low-dimensional controller commands were also very similar to those used by the ND controller. Both in terms of explained variance and rms errors ($2.4 \times 10^{-3} \pm 1.9 \times 10^{-3}$) these commands were not different from the controller using ND synergies with full-state information ($P > 0.05$, compare Fig. 3B and Fig. 4F and Fig. 4B).

Assessment of Controller Dimensionality. We also evaluated how the performance of the low-dimensional controller was affected by choosing different dimensions. This evaluation was performed by using the controller with both a low-dimensional state representation and a low-dimensional set of muscle synergies (controller 4 of Fig. 1). We found that reducing the number of dimensions from 5 to 4 resulted in a substantial degradation in controller performance (Fig. 5). In contrast, increasing the number of dimensions from 5 to 6 did not result in a significant increase in controller performance in terms of trajectories ($P > 0.05$, Fig. 5A), although there was a slight increase in performance in terms of commands ($P < 0.01$, Fig. 5B). Thus, a 5-dimensional representation offered the best tradeoff between simplifying control and maintaining efficacy.

Discussion

The basic hypothesis of using a flexible combination of a small set of motor commands for control has been proposed to explain

behaviors ranging from simple reflexes to complex voluntary movements (e.g., 8, 27, 28). However, the feasibility of such a low-dimensional controller and an underlying principle for its creation has remained elusive. In this study we proposed an explicit principle for this design: that it controls the natural dynamics of the limb that are relevant for the task being performed. The system-balancing techniques formalized this principle, allowing us to simplify the original high-dimensional, nonlinear system to a low-dimensional linear system and a set of synergies to control it. We then showed that these synergies were capable of effective control, establishing the viability of this muscle synergy hypothesis. We also showed that not any set of synergies allowed for effective control. Finally, by combining the low-dimensional model and the muscle synergies we were able to build a relatively simple controller whose performance was close to that of the best-case controller. The simplification afforded by this low-dimensional controller was evident in our analyses: solving the full-dimensional nonlinear optimal control problem by using Matlab required many hours to find a solution, whereas the low-dimensional optimal control problem took only seconds to solve. Taken together, these results establish that a low-dimensional controller is capable of simplifying control without degrading performance.

Inspection of the identified synergies showed that they created a sensible biomechanical decomposition of the musculature, with synergies focusing their actions on particular joints. We also found that these synergies were similar to some of those found during natural behaviors, whereas an alternate set of synergies, designed to span the space of joint torques, was less similar. This result was surprising, given the simplifications involved in the creation of any musculoskeletal model and the difficulty in comparing model and experimental results. These results suggest that the CNS might use a similar low-dimensional control strategy for generating movement.

The low-dimensional controller was developed in the context of controlling a particular output variable, that of the motion of joint angles. The system-balancing technique takes into account how control inputs are transformed into task outputs. The low-dimensional controller was therefore best suited for control of joint angle motion. If we had chosen a different output variable, such as the ankle motion or isometric force, the analyses used here would have resulted in a different controller and muscle synergies. This task dependence of muscle synergies is consistent with the finding of partial overlap between synergies across different behaviors in the frog (24, 29). We emphasize that this low-dimensional controller will not necessarily be the best for all possible behaviors. The creation of a low-dimensional state representation necessarily implies that aspects of the system dynamics that are not task-relevant will be excluded. Some aspects of the original system will therefore be estimated inaccurately by the low-dimensional representation. This can be viewed as both a limitation and an advantage. A single low-dimensional controller will not be adequate for all behaviors. However, low-dimensional controllers can be designed to simplify different behaviors independently, exploiting the flexibility of limb biomechanics to accomplish a range of behaviors effectively.

A related issue is that we compared controllers on a relatively idealized task: the production of point-to-point movements that minimized endpoint error and control effort. Such cost functions are common in motor control, and studies suggest that they are relevant in the production of movements (e.g., 30). However, the evaluation performed by the CNS might be whether or not the particular set of tasks it needs to produce are accomplished successfully, such as removing a noxious stimulus or escaping from a predator. For these behaviors, it is not necessarily the case that animals need to move their limb to arbitrary locations. Moreover, in such behaviors the accuracy of trajectories is not necessarily important: as long as the task is accomplished, the movement is effective (31). It is possible that if we had used a different evaluation criterion, such as the accomplishment of tasks that are ethologically

relevant, we might have found different results and potentially different synergies. It will be interesting to examine whether it is possible to develop low-dimensional controllers in the context of more natural behaviors.

Although low-dimensional controllers might arise naturally in the context of optimal control solutions (32–34), finding such solutions for high-dimensional, nonlinear systems (like the musculoskeletal system examined here) can be very difficult. In contrast, the techniques used here can be applied without initially solving the full optimal control problem. In this context, the CNS might use low-dimensional representations and muscle synergies to simplify the solution of high-dimensional optimal control problems. Such an idea is related to hierarchical controllers that have been proposed in which the CNS might use abstracted internal models of limb dynamics to translate task demands into motor commands (35–37).

In summary, the present study provides a concrete principle for specifying a low-dimensional controller: that it should be focused on the natural dynamics of the limb that are task-relevant. Given the prevalence of experimentally observed low-dimensional features in motor behaviors, this design principle may be useful for obtaining insights into biological motor control. Furthermore, given the empirical aspects of the approach described here, this principle may be useful for the design of artificial strategies for biological motor control, such as those used to restore movement after injury.

Methods

For the ND and JT synergies, we found a set of nonnegative muscle synergies, W , such that the commands could be expressed as $u(t) = \sum_i w_i c_i(t)$ where each w_i is a column of W and can be interpreted as a muscle synergy. All values of W were

constrained to be nonnegative, and $c_i(t)$ is the nonnegative command for the i th synergy. The ND synergies were chosen such that the range of possible low-dimensional limb dynamics could still be effectively excited while allowing for only nonnegative control inputs, $u(t)$. This W was derived through an iterative algorithm (see *SI Text*). To create the JT synergies, we searched for k muscle combinations, such that each combination produced a joint torque directed in one of k equally spaced directions. Accordingly, the angle between two adjacent joint torques produced by these synergies should be $360/k$ degrees. Because many muscle synergies will allow for this property, we searched for the muscle synergies that also minimized the total amount of muscle activation. This minimization resulted in a unique set of JT synergies. Note that because this optimization only specified torque directions and not magnitudes, these JT synergies might differ from those designed to optimize the feasible force set. Each controller was evaluated on 8 equally spaced targets (angular displacement of 45° in joint space) relative to the initial ankle position. The commands to the individual muscles (for the best-case controller) or to the muscle synergies (for the ND, JT, and low-dimensional controllers) necessary to move the limb to each target while minimizing the control effort were found by solving the system's Euler–Lagrange equations (e.g., 23). These differential equations, with constraints $u > 0$, were solved with the Matlab boundary value problem solver, bvp4c (see *SI Text* and **Fig. S2**). All statistical analyses were performed at the 0.05 significance level, unless stated otherwise, with Bonferroni corrections to account for multiple tests. Tests of multiple means were performed with an ANOVA followed by post hoc Bonferroni-adjusted *t* tests.

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