

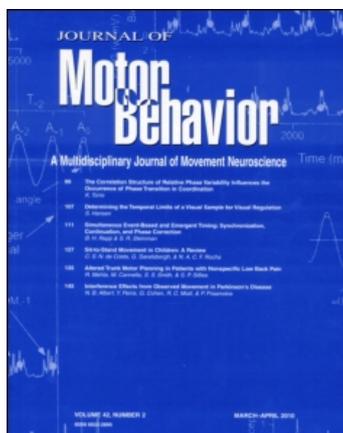
This article was downloaded by: [University Of British Columbia]

On: 23 February 2011

Access details: Access Details: [subscription number 917249060]

Publisher Routledge

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Journal of Motor Behavior

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t914957655>

### Modularity for Sensorimotor Control: Evidence and a New Prediction

Andrea d'Avella<sup>a</sup>; Dinesh K. Pai<sup>b</sup>

<sup>a</sup> Santa Lucia Foundation, Neuromotor Physiology Laboratory, Rome, Italy <sup>b</sup> Department of Computer Science, University of British Columbia, Vancouver, Canada

Online publication date: 20 November 2010

**To cite this Article** d'Avella, Andrea and Pai, Dinesh K.(2010) 'Modularity for Sensorimotor Control: Evidence and a New Prediction', Journal of Motor Behavior, 42: 6, 361 — 369

**To link to this Article:** DOI: 10.1080/00222895.2010.526453

**URL:** <http://dx.doi.org/10.1080/00222895.2010.526453>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

## RESEARCH ARTICLE

# Modularity for Sensorimotor Control: Evidence and a New Prediction

Andrea d'Avella<sup>1</sup>, Dinesh K. Pai<sup>2</sup>

<sup>1</sup>Neuromotor Physiology Laboratory, Santa Lucia Foundation, Rome, Italy. <sup>2</sup>Department of Computer Science, University of British Columbia, Vancouver, Canada.

**ABSTRACT.** By combining a few modules, the CNS may learn new control policies quickly and efficiently. Support for a modular organization of the motor system has recently come from the observation of low dimensionality in the motor commands. However, stronger evidence would come from testing the predictions on the effect of an intervention on the mechanisms required to implement a modular controller. Thus, the authors propose to test the predictions of modularity on motor adaptation. They argue that unlike a nonmodular controller, a modular controller must adapt faster to a perturbation that is compatible with the modules (i.e., one that can be compensated by reusing the same modules), than to an incompatible perturbation (i.e., one that requires new modules).

**Keywords:** hierarchical control policy, muscle synergies, motor adaptation, task perturbations

**S**ensorimotor control requires mastering the many degrees of freedom (DOF) of the musculoskeletal apparatus (i.e., generating the appropriate motor commands to achieve a goal given the state of the plant). It can be formalized as finding a (task-specific) control policy

$$\mathbf{u}(t) = \Pi(\mathbf{x}, \mathbf{g}, t).$$

That is, a mapping  $\Pi$  of a continuous state vector  $\mathbf{x}$  into time-varying motor commands  $\mathbf{u}(t)$  according to task parameters  $\mathbf{g}$  (i.e., the goal) and, in general, in a time-dependent way. For example, considering visually guided reaching with the arm,  $\mathbf{x}$  is state of the arm and its muscles,  $\mathbf{g}$  is the spatial position of the target, and  $\mathbf{u}(t)$  is the muscle activation waveforms.

How does the CNS represent and acquire such a policy? As for any mapping, it could in principle be stored in the connection weights of a neural network (possibly dynamic and recurrent). However, if the number of DOF is even moderately high, learning the appropriate weights (e.g., using a reinforcement signal) is practically impossible. Prior information on the body and the task must be used. If the CNS had an analytical model of the musculoskeletal geometry and dynamics, it could just learn the model's parameters (e.g., segments' length and inertia), plan a specific hand trajectory (desired trajectory), compute the joint angle trajectories (inverse kinematics), and use the knowledge of arm and musculoskeletal dynamics to implement a simple linear feedback controller (computed torque) that follows that trajectory. However, it is not clear how the CNS would construct an analytical model and perform the necessary computations.

Modularity may be an efficient way to incorporate and use knowledge of the body and the task to perform sensorimotor control. We define *modular control* as the construction of a control policy through a few ( $N$ ) elemental policies ( $\Phi$ ; i.e., modules or primitives) and a set of combination rules ( $\Psi$ ) depending on a few parameters ( $\alpha$ ):

$$\mathbf{u}(t) = \Psi[\{\Phi_i(\mathbf{x}, t)\}_{i=1,\dots,N}, \{\alpha_i(\mathbf{g}, \mathbf{x}, t)\}_{i=1,\dots,N}]$$

Note that the modules,  $\Phi_i$ , do not depend on the specific goal but may depend on the general task context; this is necessary for reusing the modules for different goals. For example, assuming time-invariant linear combinations of motor commands, the policy can be expressed as:

$$\mathbf{u}(t) = \sum_i c_i(\mathbf{g}) \Phi_i(\mathbf{x}, t),$$

in which  $\mathbf{u}_i(t) = \Phi_i(\mathbf{x}, t)$  is the  $i$ th elemental policy. The control  $\mathbf{u}$  could be construed directly as the muscle activation  $\mathbf{m}$ . In the case of isometric experiments the endpoint force  $\mathbf{f}$  is usually considered instead; the two are related by a state-dependent transformation. The key advantage of this approach is that, if a small number of appropriate modules  $\Phi_i$  exist, a policy for a new task can be acquired simply by learning a new low-dimensional mapping between goals ( $\mathbf{g}$ ) and modules' parameters ( $\mathbf{c}$ ). Thus, the appropriate commands in the high-dimensional motor command space are generated in a low-dimensional linear subspace. In general, the modular controller defines a nonlinear low-dimensional command manifold embedded in the high-dimensional command space.

## Learning and Modularity

In a modular controller learning is partitioned into two processes: learning the modules and learning the parameters of the modules' combination rules. The modules, incorporating knowledge of the body and the task that can be reused across task goals, may be acquired by unsupervised learning, extracting regularities from sensorimotor interactions (Todorov & Ghahramani, 2003). Once appropriate modules have been acquired, a policy can be learned efficiently using reinforcement learning or supervised learning. Thus, a

---

Correspondence address: Andrea d'Avella, Dipartimento di Fisiologia Neuromotoria, Istituto di Ricovero e Cura a Carattere Scientifico Fondazione Santa Lucia, Via Ardeatina 306, 00179, Roma, Italy. e-mail: a.davella@hsantalucia.it

modular control architecture implements a hierarchical control policy (Full & Koditschek, 1999; Ting, 2007; Todorov, Li, & Pan, 2005). Moreover, because the regularity in the musculoskeletal system captured by the modules is expected to change slowly (e.g., during development) while the acquisition of new motor skills can be rapid, it is reasonable to assume that learning the structure of the modules occurs more slowly than learning their combinations.

### Forms of Modularity

The general definition of modularity given previously can be instantiated in different ways corresponding to different types of primitives proposed for the motor system: reflexes (Sherrington, 1948), unit burst generators (Grillner, 1981), spinal force fields (Bizzi, Mussa-Ivaldi, & Giszter, 1991; Giszter, Mussa-Ivaldi, & Bizzi, 1993; Mussa-Ivaldi, Giszter, & Bizzi, 1994), small pieces of endpoint trajectories (strokes; Burdet & Milner, 1998; Flash & Henis, 1991; Krebs, Aisen, Volpe, & Hogan, 1999; Sosnik, Hauptmann, Karni, & Flash, 2004), kinematic synergies (Santello, Flanders, & Soechting, 1998), and muscle synergies (d'Avella, Saltiel, & Bizzi, 2003; Macpherson, 1991; Tresch, Saltiel, & Bizzi, 1999) or muscle modes (Krishnamoorthy, Goodman, Zatsiorsky, & Latash, 2003).

Linear combinations of force fields, specific patterns of state-dependent endpoint forces (or joint torques), have been proposed as a control mechanism implemented in the spinal cord circuitry by synchronous recruitment of muscle synergies and by force-field-preserving feedback (Giszter, Patil, & Hart, 2007):

$$\mathbf{f}(t) = \sum_i c_i(\mathbf{g}, t) \Phi_i(\mathbf{x}),$$

in which  $\mathbf{f}(t)$  are endpoint forces, the motor command  $\mathbf{u}(t)$  in this context. Assuming that the primitives depend only on the state (e.g., limb position), time-varying motor commands are generated by time-varying combination coefficients. However, these time-varying activation coefficients can also be the result of a modular control policy (e.g., by selection and combination of a few stereotypical force-field activation pulses or premotor drives).

Two models for the generation of muscle activity patterns as combination of muscle synergies have been proposed. In one model, a *time-invariant* muscle synergy is defined as a vector specifying a pattern of relative levels of muscle activations and different synergies are combined through coefficients that are state and time dependent:

$$\mathbf{m}(t) = \sum_i c_i(\mathbf{x}, \mathbf{g}, t) \mathbf{w}_i,$$

in which, in this context, the motor command  $\mathbf{u}(t)$  is the muscle activation  $\mathbf{m}(t)$ . In contrast, a *time-varying* synergy is defined as a sequence of vectors in muscle space, thus

specifying a set of muscle activation profiles, and different synergies are recruited at specific times, scaled in amplitude by scalar coefficients, and combined:

$$\mathbf{m}(t) = \sum_i c_i(\mathbf{x}, \mathbf{g}) \mathbf{w}_i(t - t_i(\mathbf{x}, \mathbf{g})).$$

Finally, focusing only on the temporal structure of the muscle patterns, muscle synergies have also been defined as groups of muscles with common activation onset and offset times identified by a clustering analysis (direct components; Krouchev, Kalaska, & Drew, 2006).

### Evidence for Modularity

The organization of the force fields recorded at the ankle in response to microstimulation of the interneuronal region of the lumbar spinal cord of spinalized frogs has provided evidence for modularity in the vertebrate motor system. Surprisingly, only a limited number types of force fields were found in a systematic stimulation of different regions of the spinal cord (Bizzi et al., 1991; Giszter et al., 1993; Saltiel, Tresch, & Bizzi, 1998). Moreover, the simultaneous stimulation of two sites, in most cases, produced a field that was the linear summation of the fields evoked from each site separately (Mussa-Ivaldi et al., 1994). Evidence for force-field summation in a natural behavior has come from the study of the corrective responses during wiping in frogs (Kargo & Giszter, 2000).

In the context of time-invariant muscle synergies, evidence for modularity has come in recent years from the analysis of the regularities in the muscle patterns recorded in several species during different behaviors (Cheung, d'Avella, & Bizzi, 2009; Cheung, d'Avella, Tresch, & Bizzi, 2005; d'Avella & Bizzi, 2005; d'Avella, Fernandez, Portone, & Lacquaniti, 2008; Hart & Giszter, 2004; Ivanenko, Poppele, & Lacquaniti, 2004; Klein Breteler, Simura, & Flanders, 2007; Krishnamoorthy et al., 2003; Saltiel, Wyler-Duda, d'Avella, Tresch, & Bizzi, 2001; Ting & Macpherson, 2005; Ting & McKay, 2007; Torres-Oviedo, Macpherson, & Ting, 2006; Torres-Oviedo, & Ting, 2007; Tresch et al., 1999). A number of decomposition algorithms (PCA, FA, NMF, ICAM; see Tresch, Cheung, & d'Avella, 2006) have been used to show that most of the variation in the muscle patterns is explained by the combination of a small number of synergies. Typically, the correct number of synergies is inferred from a change in slope (i.e., a knee) in the plot, showing the percentage of variation explained as a function of the number of synergies. Such a change in slope is interpreted as a transition between the structured variation due to the synergy combination and the unstructured variation due to noise. The fact that a small number of synergies, with respect to the number of muscles involved, is sufficient to capture a large fraction of the data variation has been interpreted as evidence for muscle synergies as modules organized by the CNS. Finally, authors of a recent simulation

study demonstrated that it is possible to build a simple low-dimensional controller combining time-invariant synergies with a performance close to that of the full-dimensional nonlinear controller (Berniker, Jarc, Bizzi, & Tresch, 2009).

Decomposition of muscle patterns using iterative optimization algorithms (d'Avella et al., 2003; d'Avella & Tresch, 2002) or PCA (Klein Breteler et al., 2007) has also provided support to time-varying muscle synergies as control modules. In freely moving, intact frogs, a large fraction of the variation in the hind limb muscle patterns recorded during natural behaviors (defensive kicking, jumping, walking, and swimming) is captured by the combinations of a few time-varying synergies, each appropriately scaled in amplitude and shifted in time (d'Avella & Bizzi, 2005; d'Avella et al., 2003). In monkeys, time-varying muscle synergies within the arm and hand muscles are modulated for reaching, grasping, and transporting objects of different shapes and sizes (Overduin, d'Avella, Roh, & Bizzi, 2008). In humans, time-varying synergies provide a parsimonious description of the shoulder and elbow muscle patterns during reaching in different directions and at different speeds (d'Avella et al., 2008; d'Avella, Portone, Fernandez, & Lacquaniti, 2006) and of hand muscle patterns during finger spelling (Klein Breteler et al., 2007). The muscle pattern description obtained with time-varying synergies is parsimonious because, given the synergies, it depends on the choice of a small number of scalar combination parameters. An insight into why simple rules for the combination of time-varying muscle synergies can be adequate for controlling movements in a variety of conditions comes from the well-known observation of the invariance of endpoint path and scaled tangential velocity for reaching at different speeds (Atkeson & Hollerbach, 1985; Morasso, 1981; Soechting & Lacquaniti, 1981). The scaling of tangential velocity along the same path can be simply obtained by scaling in amplitude (by the square of the time scale) the nongravity component of the joint torque profile (Hollerbach & Flash, 1982). Similarly, phasic time-varying muscle synergies are scaled in amplitude and time with movement speed (d'Avella et al., 2008).

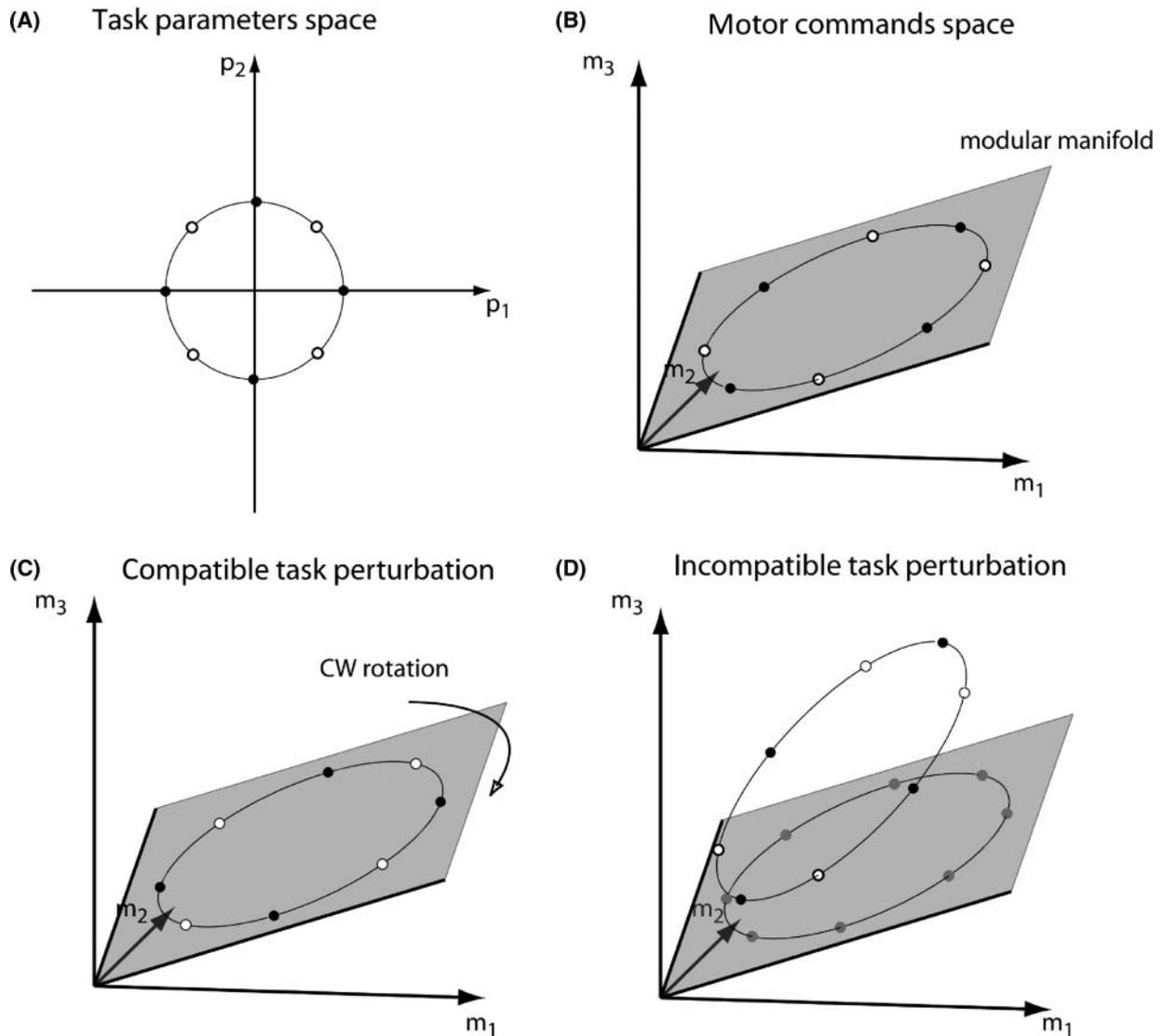
Whether the time-invariant or the time-varying synergy model best captures the modular organization of the output of the motor system is still an open question. Selective muscle vibration during targeted wiping in spinalized frogs has shown that the three muscle-activation bursts involved in the behavior are modulated independently, supporting a time-invariant rather than a time-varying model (Kargo & Giszter, 2008). However, the two models are not exclusive and may describe different functional levels in the motor system or different stages in the vertebrate phylogeny. For example, proprioceptive feedback might modulate a set of time-invariant components (Cheung et al., 2005) that are assembled into time-varying synergies by spinal central pattern generators, which in turn can be modulated by supraspinal structures.

## Critique of the Muscle Synergy Decomposition Approach

Despite the success of the decomposition approaches in explaining the muscle patterns as combinations of a few synergies, whether the observed low dimensionality simply reflects the dimensionality of the task and whether the identified synergies provide any valuable information on the organization of the motor system are important issues that need to be addressed.

Low dimensionality of the muscle patterns, indicated by the fact that a few synergies explain a large fraction of the data variation across task conditions, may simply arise from the low dimensionality of the task. Indeed, for example, the muscle patterns for a task with only one condition (e.g., reaching in one direction at a given speed) can be captured by a single time-varying synergy corresponding to the patterns averaged over repetitions. Clearly, the intertrial variation is not accounted for by a model describing the variation across task conditions and it may or may not be captured by synergies (Kutch, Kuo, Bloch, & Rymer, 2008; Valero-Cuevas, Venkadesan, & Todorov, 2009). However, if there is substantial variability in the task conditions and they are sampled appropriately, the dimensionality of the muscle patterns is potentially much higher than the dimensionality of the task and low dimensionality of the patterns represents a significant observation. Considering for simplicity static motor output (e.g., the production of a constant isometric force on a handle), if task conditions are described by  $D$  parameters (e.g., for  $D = 2$  the production of an arbitrary force on a plane) and  $M$  muscles are involved in the task, with  $M$  in general higher than  $D$ , the control policy is represented by a mapping from task parameter space to muscle space whose image is a  $D$ -dimensional manifold. Such a manifold, in general, need not be embedded in any proper subspace of the muscle space, and may be embedded in the whole space (i.e., have dimensionality  $M$ ). If considering dynamic motor output, even if we discretize time at low frequency, the dimensionality of the motor command space is the product of  $M$  times the number of time samples and thus much higher than  $D$ .

The fact that synergy combinations capture the muscle pattern variations across task conditions indicates that the synergy model is capable of describing the control policy used by the CNS. However, the decomposition approach provides a descriptive model of the control policy and not a causal model (i.e., a model of the mechanisms that implements the policy). The problem is not simply with the need for data fitting, necessary for any model that depends on some parameters. In fact, once the synergies are identified from some data, they can explain the organization of new data (d'Avella et al., 2006; Torres-Oviedo et al., 2006; i.e., they generalize). However, to test a causal model it is necessary to test a prediction of an intervention affecting its mechanisms.

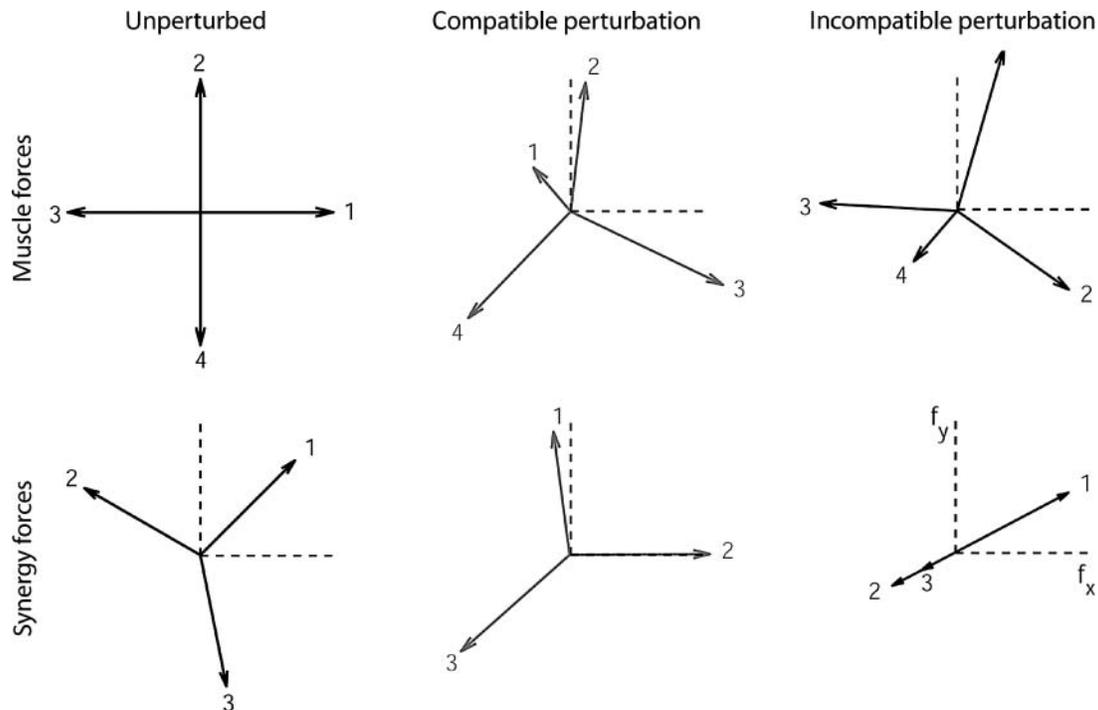


**FIGURE 1.** Task perturbations that are compatible or incompatible with the modular organization of a controller: an example with a hypothetical simple task and musculoskeletal system. **(A)** Consider, for illustration, eight specific conditions arranged on a circle in parameters space of a task characterized by two parameters. For example, the parameters might represent the location on a plane of the target of a reaching movement. **(B)** Assume that the motor commands generated by the controller to perform the task lie on a proper subspace of the motor command space, such as a plane (modular manifold) in three-dimensional space. **(C)** A compatible perturbation of the task is one that can be compensated by generating new motor commands still on the manifold (i.e., by recombining existing modules). One simple example is a rotation of the motor commands within the manifold. **(D)** An incompatible perturbation can only be compensated by mapping the task parameters into new motor commands off the manifold. If the controller is modular (i.e., constrained to generate motor commands on a manifold) adapting to an incompatible task perturbation requires adjusting the structure of the modules, a process that likely occurs more slowly than the adjustment of the modules' combinations. Thus, differences in learning difficulty during adaptation to compatible and incompatible task perturbations discriminates between modular and nonmodular controllers.

### A New Prediction of Modularity on Motor Adaptation

The approach that we are presently pursuing to test modularity as a causal model is grounded on the following observation. As modularity allows efficient learning of control

policies by reducing the number of parameters it also constrains the policies that can be learned with the modules (i.e., there is no free lunch). Thus, policies implemented with modules may be suboptimal. Specifically, modular policies may be suboptimal for adapting to perturbations of the task



**FIGURE 2.** An example of compatible and incompatible perturbations in a simple system. An idealized musculoskeletal system with two degrees of freedom (DOF;  $x$  and  $y$ ) has two pairs of antagonist muscles for each DOF generating isometric forces along the axes of the output force space (top left panel). A modular controller recruits the four muscles through three muscle synergies, each generating a specific force (bottom left panel). Both compatible and incompatible perturbations are obtained by changing the force generated by each one of the four muscles and thus changing the forces generated by the activation of the synergies. However, only in the case of an incompatible perturbation the forces generated by the synergies are collinear, thus making the synergies unable to span the force space.

conditions that are incompatible with the modules (i.e., that cannot be compensated by recombining existing modules). Suppose task perturbations that require similar adjustments of the motor commands but are either compatible or incompatible with the modules identified by decomposition methods. If the modules are not simply a descriptive tool but are organized by the CNS, we predict that the adaptation process will be more difficult for incompatible perturbations than for compatible ones.

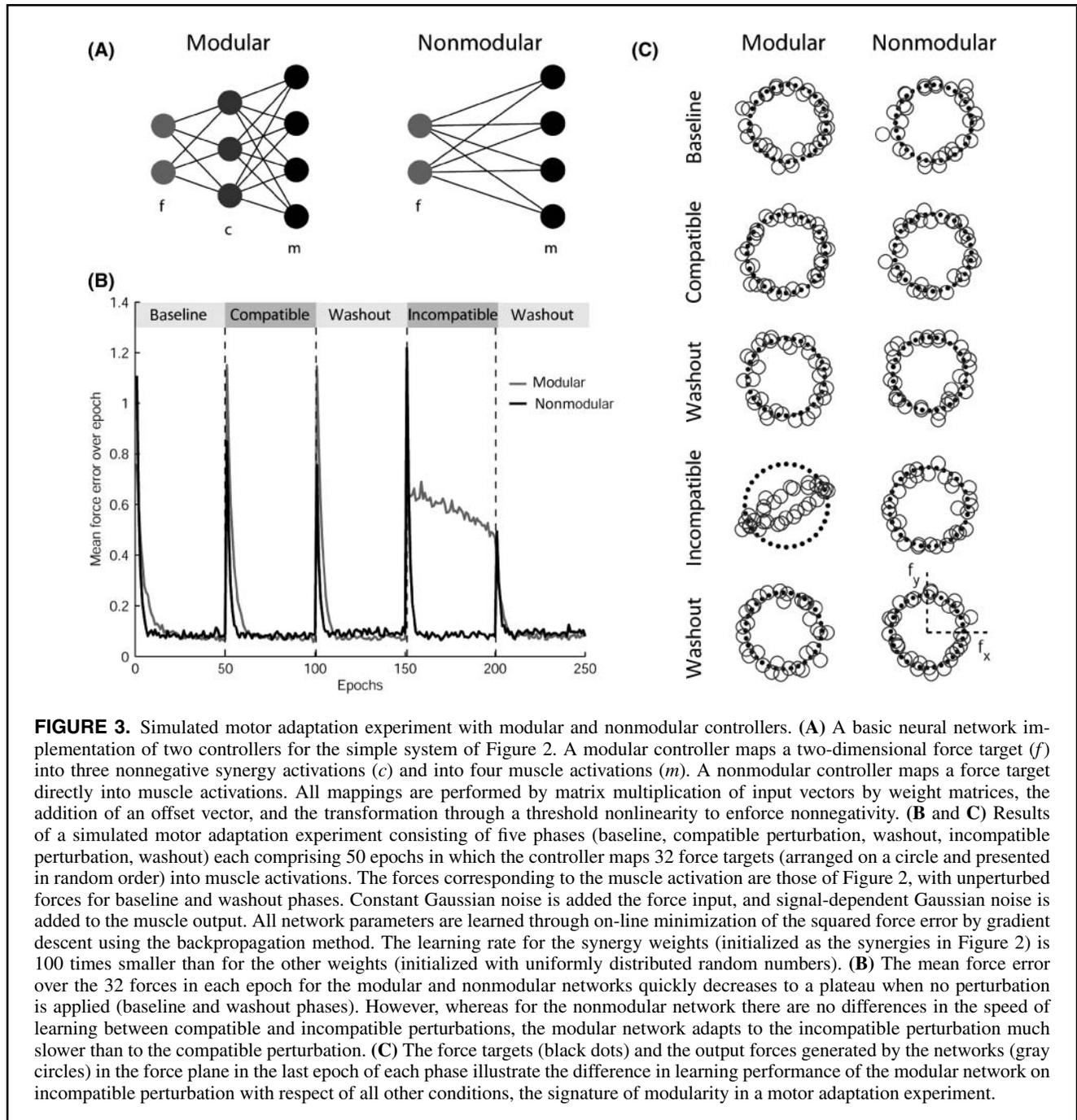
Consider a task (see the example in Figure 1) characterized by  $D$  parameters (e.g., the spatial location of a reach target; two parameters are illustrated in the figure) and assume that the observed motor commands for solving the task lie on a linear manifold of dimension  $N$ , with  $N < M$ , number of muscles (shown as a plane in a three-dimensional motor command space in the example). The low dimensionality of the motor command manifold suggests that it is the result of the combination of a few modules organized by the CNS but does not exclude alternative explanations. However, we claim that it is possible to distinguish experimentally this explanation from the alternative explanation that the motor commands are not generated by a modular controller and the

linear manifold is simply a description of the solution found by the nonmodular controller.

Suppose the controller is modular and the modules are learned or adjusted more slowly than the mapping between task parameters and modules' combination coefficients. We argue that in this case the adaptation to a compatible perturbation (i.e., one that can be compensated by reusing existing modules) is faster than adaptation to an incompatible perturbation (i.e., one that requires learning new modules). In contrast, if the controller is not modular and the observed low-dimensional manifold is simply a description of the solution and not caused by the controller's architecture, we would expect no difference in the adaptation rates if the changes in motor commands required to adapt to the two types of perturbations are comparable.

### A Simulated Adaptation Experiment with a Simple System

To illustrate how the prediction of modularity can be tested in a motor adaptation experiment, we consider a very simple and idealized musculoskeletal system with two



**FIGURE 3.** Simulated motor adaptation experiment with modular and nonmodular controllers. **(A)** A basic neural network implementation of two controllers for the simple system of Figure 2. A modular controller maps a two-dimensional force target ( $f$ ) into three nonnegative synergy activations ( $c$ ) and into four muscle activations ( $m$ ). A nonmodular controller maps a force target directly into muscle activations. All mappings are performed by matrix multiplication of input vectors by weight matrices, the addition of an offset vector, and the transformation through a threshold nonlinearity to enforce nonnegativity. **(B and C)** Results of a simulated motor adaptation experiment consisting of five phases (baseline, compatible perturbation, washout, incompatible perturbation, washout) each comprising 50 epochs in which the controller maps 32 force targets (arranged on a circle and presented in random order) into muscle activations. The forces corresponding to the muscle activation are those of Figure 2, with unperturbed forces for baseline and washout phases. Constant Gaussian noise is added to the force input, and signal-dependent Gaussian noise is added to the muscle output. All network parameters are learned through on-line minimization of the squared force error by gradient descent using the backpropagation method. The learning rate for the synergy weights (initialized as the synergies in Figure 2) is 100 times smaller than for the other weights (initialized with uniformly distributed random numbers). **(B)** The mean force error over the 32 forces in each epoch for the modular and nonmodular networks quickly decreases to a plateau when no perturbation is applied (baseline and washout phases). However, whereas for the nonmodular network there are no differences in the speed of learning between compatible and incompatible perturbations, the modular network adapts to the incompatible perturbation much slower than to the compatible perturbation. **(C)** The force targets (black dots) and the output forces generated by the networks (gray circles) in the force plane in the last epoch of each phase illustrate the difference in learning performance of the modular network on incompatible perturbation with respect of all other conditions, the signature of modularity in a motor adaptation experiment.

mechanical DOF and four muscles generating static isometric forces through a linear mapping of nonnegative muscle activation. The task consists of generating a two-dimensional force vector  $\mathbf{f}$ , through the muscle-to-force transformation matrix  $\mathbf{H}$  (determined by the geometry and biomechanical characteristics of the system, see Figure 2),  $\mathbf{f} = \mathbf{H} \mathbf{m}$ , matching arbitrary target forces  $\mathbf{f}^*$  in the feasible force set and available via sensory input. We consider a modular controller implementing a control policy by mapping a force target into a nonnegative linear combi-

nation of three time-invariant muscle synergies,  $\mathbf{m} = [\mathbf{W}\mathbf{c}]_+$ ,  $\mathbf{c} = [\mathbf{A}\mathbf{f}^* + \mathbf{a}]_+$ , with  $\mathbf{W}$  the synergy matrix of dimensions  $4 \times 3$ ,  $\mathbf{c}$  the synergy combination coefficient vector,  $\mathbf{A}$  and  $\mathbf{a}$  the matrix and offset vector mapping force targets into synergy coefficients, respectively, and  $[\ ]_+$  positive part function to enforce nonnegativity. If the synergy matrix is chosen appropriately (e.g., the columns of  $\mathbf{W}$  illustrated by arrows in the bottom left panel of Figure 2), it spans the force space by nonnegative synergy combinations. We also consider a nonmodular controller mapping

directly force targets into muscle activations,  $\mathbf{m} = [\mathbf{B}\mathbf{f}^* + \mathbf{b}]_+$ , with  $\mathbf{B}$  and  $\mathbf{b}$  mapping matrix and offset vector, respectively.

In a simulated experiment with the two controllers, once the task has been learned (i.e., the modular controller has acquired adequate  $\mathbf{W}$ ,  $\mathbf{A}$ , and  $\mathbf{a}$  and the nonmodular controller has acquired  $\mathbf{B}$  and  $\mathbf{b}$ , minimizing the error  $\|\mathbf{H}\mathbf{m} - \mathbf{f}^*\|^2$ ), the rates of adaptation to perturbations compatible and incompatible with the synergies  $\mathbf{W}$  are compared. In both cases the perturbations are obtained by changing the force generated by each one of the four muscles (i.e., transforming the matrix  $\mathbf{H}$ , illustrated in Figure 2 by the arrows in the top left panel). With an incompatible perturbation the forces associated with the synergies change so that they are unable to span the force space by nonnegative combinations (e.g., bottom right panel in Figure 2). In contrast, with a compatible perturbation the forces associated with the synergies change but they can still span by nonnegative combinations the force space (e.g., bottom-middle panel).

Both modular and nonmodular controllers must adjust the mapping of target forces to synergy ( $\mathbf{A}$  and  $\mathbf{a}$ ) or muscle ( $\mathbf{B}$  and  $\mathbf{b}$ ) activations to adapt to both types of perturbations. However, the modular controller must also adjust the synergies ( $\mathbf{W}$ ) in the case of incompatible perturbations and such an adaptation process is likely to occur with a lower learning rate than the other adaptation processes. Thus, a modular controller adapts more slowly to an incompatible than to a compatible one, whereas a nonmodular controller adapts with similar rates.

Figure 3 illustrates a simulated experiment with a simple neural network implementation of the modular and nonmodular controllers (Figure 3A) learning to generate 32 force targets arranged on a unit circle and adapting to the two perturbations of Figure 2. The learning rate of the modular network is clearly distinguishable from the nonmodular during the adaptation to the incompatible perturbation.

### Compatible and Incompatible Perturbations in a Real Motor Task

Testing the prediction that perturbations that are incompatible with the modular control architecture are harder to compensate than compatible perturbations in a real motor task requires choosing a specific type of module, such as time-invariant or time-varying muscle synergies, identifying the set of specific instances of the module that best capture the control of the task in an individual subject, and constructing subject-specific perturbations according to those instances. In an isometric manipulation task, perturbations compatible and incompatible with a set of time-invariant synergies may be generated by remapping the force generated by each synergy at the end effector. Although this could be done by mechanically altering the relationship between muscle activations and the force generated at the end effector, these remappings may be performed more flexibly in a virtual environment providing the appropriate visual feedback through a simula-

tion. Such simulation may require a detailed musculoskeletal model (Delp et al., 2007; Sueda, Kaufman, & Pai, 2008) to estimate the end-effector forces associated with the synergies. In a movement task such as reaching, the joint torque profiles generated by a set of time-varying synergies, which parsimoniously capture the regularities in the motor output (d'Avella et al., 2006) would have to be remapped into novel torque profiles. In case of an incompatible perturbation the remapped torque profiles of two synergies cancel each other, generating a motor impairment that requires changing the synergy structure. As such, instead of physically remapping muscle to endpoint forces, the perturbation may be performed on a simulated arm in a virtual environment with visual and haptic feedback.

### Conclusion

Building control policies by combining a few control modules may be how the CNS solves the challenging problem of mastering the many DOF of the musculoskeletal system inherent in sensorimotor control. Incorporating knowledge of the body and the task into a limited number of modules may allow efficient implementation of an adequate control policy as a low-dimensional mapping between task parameters and module combination parameters. In such a hierarchical control architecture, learning a new task or adapting to a novel perturbation may be accomplished by two separate processes operating on different time scales. Appropriate module combinations may be learned quickly and efficiently through error or reinforcement signals. When needed, new modules may be slowly acquired or existing modules slowly adjusted by unsupervised learning. However, to date, evidence for modularity is indirect because it mainly relies on the observations of low dimensionality in the motor output more than on a test of modularity as a causal model. Such a test requires a prediction of the effect of an intervention on mechanisms that implement the control policy. We thus propose to test a specific prediction of modularity on the difficulty of motor adaptation. If the modules identified from the observed regularities of the motor output were a mere description of those regularities, unrelated to the implementation of the controller, we predict that there would be no difference in the difficulty in compensating a perturbation that requires recombining the existing modules (compatible) or one that requires new modules (incompatible). In contrast, if the modules capture the controller's actual mechanisms, we predict that adapting to an incompatible perturbation would be more difficult than adapting to a compatible perturbation that is similar in terms of the required changes in the motor commands. In sum, we have identified a novel experimental approach for testing a causal prediction of modularity.

### ACKNOWLEDGMENTS

The authors thank Michele Andrea Pisauro for help with the neural network simulation and Reinhard Gentner for comments on the manuscript. This work was supported by a Research Grant of

the Human Frontier Science Program Organization awarded to A. d'Avella and D. P. (RGP11/2008).

## REFERENCES

- Atkeson, C. G., & Hollerbach, J. M. (1985). Kinematic features of unrestrained vertical arm movements. *Journal of Neuroscience*, *5*, 2318–2330.
- Berniker, M., Jarc, A., Bizzi, E., & Tresch, M. C. (2009). Simplified and effective motor control based on muscle synergies to exploit musculoskeletal dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 7601–7606.
- Bizzi, E., Mussa-Ivaldi, F. A., & Giszter, S. F. (1991). Computations underlying the execution of movement: A biological perspective. *Science*, *253*, 287–291.
- Burdet, E., & Milner, T. E. (1998). Quantization of human motions and learning of accurate movements. *Biological Cybernetics*, *78*, 307–318.
- Cheung, V. C., d'Avella, A., & Bizzi, E. (2009). Adjustments of motor pattern for load compensation via modulated activations of muscle synergies during natural behaviors. *Journal of Neurophysiology*, *101*, 1235–1257.
- Cheung, V. C., d'Avella, A., Tresch, M. C., & Bizzi, E. (2005). Central and sensory contributions to the activation and organization of muscle synergies during natural motor behaviors. *Journal of Neuroscience*, *25*, 6419–6434.
- d'Avella, A., & Bizzi, E. (2005). Shared and specific muscle synergies in natural motor behaviors. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 3076–3081.
- d'Avella, A., Fernandez, L., Portone, A., & Lacquaniti, F. (2008). Modulation of phasic and tonic muscle synergies with reaching direction and speed. *Journal of Neurophysiology*, *100*, 1433–1454.
- d'Avella, A., Portone, A., Fernandez, L., & Lacquaniti, F. (2006). Control of fast-reaching movements by muscle synergy combinations. *Journal of Neuroscience*, *26*, 7791–7810.
- d'Avella, A., Saltiel, P., & Bizzi, E. (2003). Combinations of muscle synergies in the construction of a natural motor behavior. *Nature Neuroscience*, *6*, 300–308.
- d'Avella, A., & Tresch, M. C. (2002). Modularity in the motor system: Decomposition of muscle patterns as combinations of time-varying synergies. In T. G. Dietterich, S. Becker & Z. Ghahramani (Eds.), *Advances in neural information processing systems 14* (pp. 141–148). Cambridge, MA: MIT Press.
- Delp, S. L., Anderson, F. C., Arnold, A. S., Loan, P., Habib, A., John, C. T., et al. (2007). OpenSim: Open-source software to create and analyze dynamic simulations of movement. *IEEE Transactions on Biomedical Engineering*, *54*, 1940–1950.
- Flash, T., & Henis, E. (1991). Arm trajectory modifications during reaching towards visual targets. *Journal of Cognitive Neuroscience*, *3*, 220–230.
- Full, R. J., & Koditschek, D. E. (1999). Templates and anchors: Neuro-mechanical hypotheses of legged locomotion on land. *Journal of Experimental Biology*, *202*, 3325–3332.
- Giszter, S. F., Mussa-Ivaldi, F. A., & Bizzi, E. (1993). Convergent force fields organized in the frog's spinal cord. *Journal of Neuroscience*, *13*, 467–491.
- Giszter, S. F., Patil, V., & Hart, C. (2007). Primitives, premotor drives, and pattern generation: A combined computational and neuroethological perspective. *Progress in Brain Research*, *165*, 323–346.
- Grillner, S. (1981). Control of locomotion in bipeds, tetrapods, and fish. In V. B. Brooks (Ed.), *Handbook of physiology: Sect 1. The nervous system* (Vol. 2., pp. 1179–1236). Bethesda, MD: American Physiological Society.
- Hart, C. B., & Giszter, S. F. (2004). Modular premotor drives and unit bursts as primitives for frog motor behaviors. *Journal of Neuroscience*, *24*, 5269–5282.
- Hollerbach, M. J., & Flash, T. (1982). Dynamic interactions between limb segments during planar arm movement. *Biological Cybernetics*, *44*, 67–77.
- Ivanenko, Y. P., Poppele, R. E., & Lacquaniti, F. (2004). Five basic muscle activation patterns account for muscle activity during human locomotion. *Journal of Physiology*, *556*, 267–282.
- Kargo, W. J., & Giszter, S. F. (2000). Rapid correction of aimed movements by summation of force-field primitives. *Journal of Neuroscience*, *20*, 409–426.
- Kargo, W. J., & Giszter, S. F. (2008). Individual premotor drive pulses, not time-varying synergies, are the units of adjustment for limb trajectories constructed in spinal cord. *Journal of Neuroscience*, *28*, 2409–2425.
- Klein Breteler, M. D., Simura, K. J., & Flanders, M. (2007). Timing of muscle activation in a hand movement sequence. *Cerebral Cortex*, *17*, 803–815.
- Krebs, H. I., Aisen, M. L., Volpe, B. T., & Hogan, N. (1999). Quantization of continuous arm movements in humans with brain injury. *Proceedings of the National Academy of Sciences of the United States of America*, *96*, 4645–4649.
- Krishnamoorthy, V., Goodman, S., Zatsiorsky, V., & Latash, M. L. (2003). Muscle synergies during shifts of the center of pressure by standing persons: Identification of muscle modes. *Biological Cybernetics*, *89*, 152–161.
- Krouchev, N., Kalaska, J. F., & Drew, T. (2006). Sequential activation of muscle synergies during locomotion in the intact cat as revealed by cluster analysis and direct decomposition. *Journal of Neurophysiology*, *96*(4), 1991–2010.
- Kutch, J. J., Kuo, A. D., Bloch, A. M., & Rymer, W. Z. (2008). Endpoint force fluctuations reveal flexible rather than synergistic patterns of muscle cooperation. *Journal of Neurophysiology*, *100*, 2455–2471.
- Macpherson, J. M. (1991). How flexible are muscle synergies? In D. R. Humphrey & H.-J. Freund (Eds.), *Motor control: Concepts and issues* (pp. 33–47). Chichester, England: Wiley.
- Morasso, P. (1981). Spatial control of arm movements. *Experimental Brain Research*, *42*, 223–227.
- Mussa-Ivaldi, F. A., Giszter, S. F., & Bizzi, E. (1994). Linear combinations of primitives in vertebrate motor control. *Proceedings of the National Academy of Science*, *91*, 7534–7538.
- Overduin, S. A., d'Avella, A., Roh, J., & Bizzi, E. (2008). Modulation of muscle synergy recruitment in primate grasping. *Journal of Neuroscience*, *28*, 880–892.
- Saltiel, P., Tresch, M. C., & Bizzi, E. (1998). Spinal cord modular organization and rhythm generation: An NMDA iontophoretic study in the frog. *Journal of Neurophysiology*, *80*, 2323–2339.
- Saltiel, P., Wyler-Duda, K., D'Avella, A., Tresch, M. C., & Bizzi, E. (2001). Muscle synergies encoded within the spinal cord: Evidence from focal intraspinal NMDA iontophoresis in the frog. *Journal of Neurophysiology*, *85*, 605–619.
- Santello, M., Flanders, M., & Soechting, J. F. (1998). Postural hand synergies for tool use. *Journal of Neuroscience*, *18*, 10105–10115.
- Sherrington, C. S. (1948). *The integrative action of the nervous system*. Cambridge: University Press.
- Soechting, J. F., & Lacquaniti, F. (1981). Invariant characteristics of a pointing movement in man. *Journal of Neuroscience*, *1*, 710–720.
- Sosnik, R., Hauptmann, B., Karni, A., & Flash, T. (2004). When practice leads to co-articulation: The evolution of geometrically defined movement primitives. *Experimental Brain Research*, *156*, 422–438.

- Sueda, S., Kaufman, A., & Pai, D. K. (2008). Musculotendon simulation for hand animation. *ACM Transactions on Graphics*, 27, 1–8. doi:10.1145/1360612.1360682
- Ting, L. H. (2007). Dimensional reduction in sensorimotor systems: A framework for understanding muscle coordination of posture. *Progress in Brain Research*, 165, 299–321.
- Ting, L. H., & Macpherson, J. M. (2005). A limited set of muscle synergies for force control during a postural task. *Journal of Neurophysiology*, 93, 609–613.
- Ting, L. H., & McKay, J. L. (2007). Neuromechanics of muscle synergies for posture and movement. *Current Opinion in Neurobiology*, 17, 622–628.
- Todorov, E., & Ghahramani, Z. (2003). *Unsupervised learning of sensory-motor primitives*. Paper presented at the IEEE Engineering in Medicine, and Biology Society.
- Todorov, E., Li, W., & Pan, X. (2005). From task parameters to motor synergies: A hierarchical framework for approximately-optimal control of redundant manipulators. *Journal of Robotic Systems*, 22, 691–710.
- Torres-Oviedo, G., Macpherson, J. M., & Ting, L. H. (2006). Muscle synergy organization is robust across a variety of postural perturbations. *Journal of Neurophysiology*, 96, 1530–1546.
- Torres-Oviedo, G., & Ting, L. H. (2007). Muscle synergies characterizing human postural responses. *Journal of Neurophysiology*, 98, 2144–2156.
- Tresch, M. C., Cheung, V. C., & d'Avella, A. (2006). Matrix factorization algorithms for the identification of muscle synergies: evaluation on simulated and experimental data sets. *Journal of Neurophysiology*, 95, 2199–2212.
- Tresch, M. C., Saltiel, P., & Bizzi, E. (1999). The construction of movement by the spinal cord. *Nature Neuroscience*, 2, 162–167.
- Valero-Cuevas, F. J., Venkadesan, M., & Todorov, E. (2009). Structured variability of muscle activations supports the minimal intervention principle of motor control. *Journal of Neurophysiology*, 102, 59–68.

Submitted July 31, 2009  
Accepted August 31, 2010