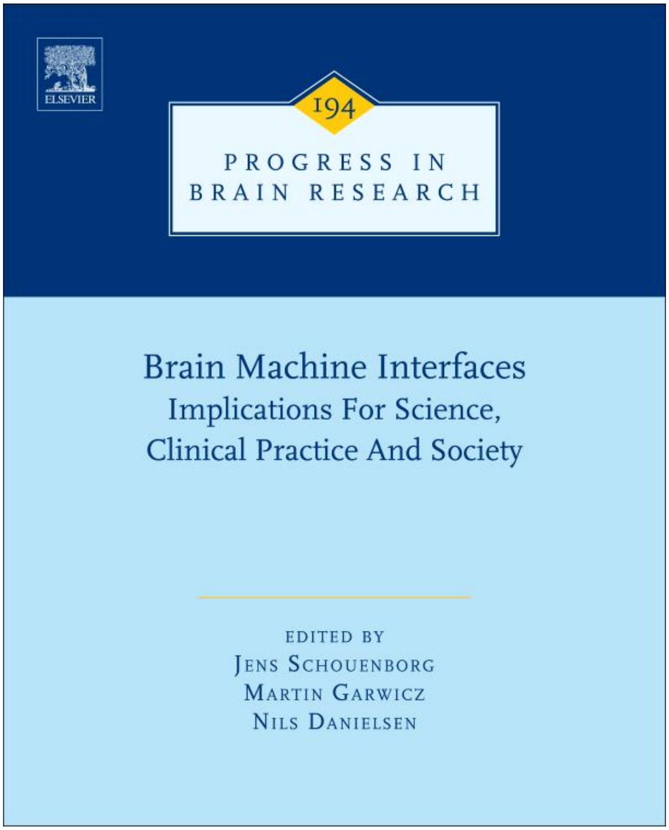

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PROGRESS IN BRAIN RESEARCH

Brain Machine Interfaces
Implications For Science,
Clinical Practice And Society

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CHAPTER 15

Modeling the potentiality of spinal-like circuitry for stabilization of a planar arm system

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Abstract: The design of control systems for limb prostheses seems likely to benefit from an understanding of how sensorimotor integration is achieved in the intact system. Traditional BMIs guess what movement parameters are encoded by brain activity and then decode them to drive prostheses directly. Modeling the known structure and emergent properties of the biological decoder itself is likely to be more effective in bridging from normal brain activity to functionally useful limb movement. In this study, we have extended a model of spinal circuitry (termed SLR for spinal-like regulator; see Raphael, G., Tsianos, G. A., & Loeb G. E. 2010, Spinal-like regulator facilitates control of a two-degree-of-freedom wrist. *The Journal of Neuroscience*, *30*(28), 9431–9444.) to a planar elbow–shoulder system to investigate how the spinal cord contributes to the control of a musculoskeletal system with redundant and multiarticular musculature and interaction (Coriolis) torques, which are common control problems for multisegment linkages throughout the body. The SLR consists of a realistic set of interneuronal pathways (monosynaptic Ia-excitatory, reciprocal Ia-inhibitory, Renshaw inhibitory, Ib-inhibitory, and propriospinal) that are driven by unmodulated step commands with learned amplitudes. We simulated the response of a planar arm to a brief, oblique impulse at the hand and investigated the role of cocontraction in learning to resist it. Training the SLR without cocontraction led to generally poor performance that was significantly worse than training with cocontraction. Further, removing cocontraction from the converged solutions and retraining the system achieved better performance than the SLR responses without cocontraction. Cocontraction appears to reshape the solution space, virtually eliminating the probability of entrapment in poor local minima. The local minima that are entered during learning with cocontraction are favorable starting points for learning to perform the task when cocontraction is abruptly removed. Given the control system's ability to learn effectively and rapidly, we hypothesize that it will generalize more readily to the wider range of tasks that subjects must learn to perform, as opposed to BMIs mapped to outputs of the musculoskeletal system.

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Introduction

Moving limbs in a purposeful manner, whether it is a simple reaching movement or fine manipulation of an object, is an elaborate process that requires sophisticated integration of volitional commands and sensory feedback. The design of control systems for sensorimotor prostheses seems likely to benefit from an understanding of how such control is achieved in the intact system. Many regions of the brain participate in this process, but all of their output signals are integrated in the spinal cord. The spinal circuitry consists of a variety of reasonably well-characterized interneurons that are highly evolved and conserved throughout mammalian and even vertebrate evolution (Pierrot-Deseilligny and Burke, 2005). In particular, the large majority of corticospinal neurons have few or no direct projections to spinal motoneurons (Rathelot and Strick, 2009), projecting instead to spinal interneurons where their signals are integrated with various somatosensory afferents and recurrent motoneuron signals. Depending on one's perspective, any given muscle recruitment can be described either as the result of a descending command that has been modulated by segmental feedback or a segmental reflex whose gain has been set by descending commands; given the circuitry, they are functionally indistinguishable.

A brain–machine interface naturally focuses on the cortical command signals. Cortical activity recorded from nonhuman primates during trained motor behaviors can be correlated with experimental measures of the kinematics or kinetics of the performance. The decoded cortical signals can be used to recreate those kinematics or kinetics in a robotic or virtual simulation of the limb (see other chapters in this volume). Because of the mechanical coupling within the musculoskeletal system, however, similar correlations can be obtained with a wide variety of measures of the task (Churchland and Shenoy, 2007). Further, the input–output relationships shift substantially with small changes to the task (e.g., changes in limb posture unrelated to the end-point trajectory being controlled; Scott and Kalaska, 1997). This suggests that the dimensionality of neural activity is significantly larger than the set of movement parameters that are hypothesized to be encoded (see Churchland and Shenoy, 2007). This also indicates that the correlations do not reflect the coordinate frame in which the brain normally computes command signals. Further, these correlations may actually reflect cortical inputs from higher motor planning centers (e.g., parietal cortex) and/or somatosensory feedback and efference-copy signals from lower centers such as the spinal cord.

Rather than guessing what coordinates the brain might use and building decoders based on correlations observed, we can start with the known structure of the biological decoder itself. Fortunately, a fair amount of spinal connectivity is known (see Jankowska, 1992; Pierrot-Deseilligny and Burke, 2005). Modeling of musculoskeletal systems is sufficiently advanced to support the development of realistic model systems in which the potentiality of the components can be appreciated. Modeling tools can be used to gain insight into the spinal cord's contribution to various behavioral phenomena such as kinematic performance, stability, energy consumption, and learning. Alternatively, they can also give us insight into the extent to which these aspects need to be specified explicitly by higher centers or treated as emergent properties of the system being controlled.

In previous research, we obtained surprising results from a realistic model of the spinal circuitry operating a model of a two degree-of-freedom wrist with four muscles (Raphael et al., 2010). The model consisted of a realistic set of interneurons whose descending commands were simple step functions with learned amplitudes.

The model was called a "spinal-like regulator" (SLR) because it included elements that may actually be located in supraspinal circuits and excluded some known spinal interneurons whose connectivity or roles were less well characterized. Despite having an oversimplified brain whose outputs were limited to unmodulated steps, learning by adjusting one gain at a time rapidly discovered physiological solutions for a wide range of tasks. Even with a large number of control inputs, the simple learning algorithm always converged rapidly to solutions similar to published normal behavior regardless of the random starting point of the search. This is surprising because the large number of control inputs would theoretically create a complex solution space with many undesirable local minima. The fact that training always resulted in good performance implies that the structure of the spinal circuitry facilitates learning by crafting a solution space consisting of many local minima that are good enough for many common tasks. Further, details of muscle activity during the learned behaviors appeared to be physiological (e.g., minimal cocontraction) even though muscle activation was not included in the training criteria. This suggested that the structure of the spinal cord is predisposed toward metabolically efficient behavior.

In this study, we have extended this modeling scheme to a planar elbow–shoulder system to investigate how the spinal cord contributes to the control of a musculoskeletal system with redundant and multiarticular musculature and interaction (Coriolis) torques, which are common control problems for multisegment linkages throughout the body.

Methods

Simulation environment

The neuromusculoskeletal system shown schematically in Fig. 1 includes realistic models of muscles, proprioceptors, and spinal circuitry in conjunction with a simplified model of the brain. Models of individual components have been described in other publications and are summarized here.

Musculoskeletal model

The musculoskeletal system represents an arm whose motion is constrained within the horizontal plane (see Brown and Loeb, 2000). The three-segment skeleton is made up of torso, upper and lower arm segments that are linked by hinge-like shoulder and elbow joints. Each joint is operated by a pair of antagonist muscles that provide flexion and extension torques. In addition, a pair of biarticular muscles provides flexion and extension torques across both muscles. See Fig. 2 for a detailed description of the musculoskeletal parameters.

The muscle model used in this study (Tsianos et al., 2011, in preparation) is a modified version of virtual muscle (VM) presented in Cheng et al. (2000). The new muscle model is more computationally efficient and computes energy consumption in addition to force over a wide range of stimulation conditions. It accurately captures the nonlinear effects of firing rate, kinematics, and fiber composition on force production and energy consumption. Tendon plus aponeurosis are modeled as a nonlinear elastic component in series with the contractile machinery. Under dynamic conditions, such series elasticity results in substantial differences between the kinematics of the whole muscle and of the muscle fascicles and spindles, which have significant effects on force production, energy consumption, and proprioceptor activity.

Proprioceptor models

Each muscle in our system includes models of muscle spindles (Mileusnic et al., 2006) and Golgi tendon organs (GTO; Mileusnic and Loeb, 2009). The muscle spindle model generates a response depending on fascicle kinematics and fusimotor excitation, with separate gamma static and gamma dynamic control of length and velocity

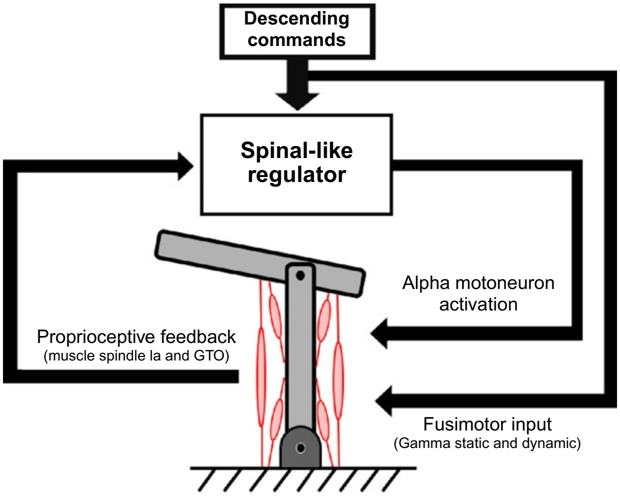
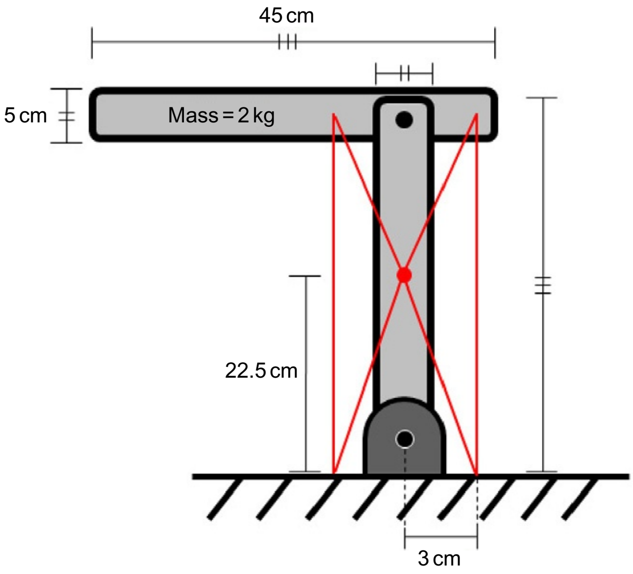


Fig. 1. Schematic overview of the neuromusculoskeletal system of a planar arm. Descending commands from the brain model and proprioceptive feedback from muscle spindle and Golgi tendon organ models project to interneurons in the spinal-like regulator (SLR). The interneurons integrate this information and send it to the alpha motoneurons that drive the muscles. The brain model also delivers fusimotor input to the muscle spindles, effectively setting their transduction sensitivity.



Muscle properties

	Monoarticular	Biarticular
Optimal fascicle length (cm)	8.5	25
Fascicle length: tendon length	2:1	1:1
Optimal force (*N*)	1400	1000

Fig. 2. Musculoskeletal system parameters. The proximal and distal arms have identical dimensions and mass, which is uniformly distributed over each segment. In the posture shown in the figure, the muscles are arranged symmetrically about the proximal segment. The monoarticular muscles have one attachment point at the center of the proximal segment and another one 3 cm away from the joint they actuate. The biarticular muscles attach 3 cm away from the elbow and shoulder joint on the same side of the proximal segment.

sensitivity, respectively. Although the model captures both group Ia and II afferent responses, we used only the Ia response in our system because we omitted spinal circuitry associated with group II feedback (see Raphael et al., 2010). The GTO model generates a response that represents activity from an ensemble of group Ib afferents in response to whole muscle tension.

Spinal cord model

The spinal cord model is composed of classical interneuronal circuitry described in the experimental literature plus fusimotor control for the muscle spindles. It includes the following pathways: monosynaptic Ia-excitatory, reciprocal Ia-inhibitory, Renshaw inhibitory, Ib-inhibitory, and propriospinal interneuronal pathways. These circuits between a given pair of muscles are largely defined by their functional relationship, which can be synergist, antagonist, or variable depending on task, which we term partial synergists. The connectivity of these relationships for each type of interneuronal circuit is described in detail in Raphael et al. (2010).

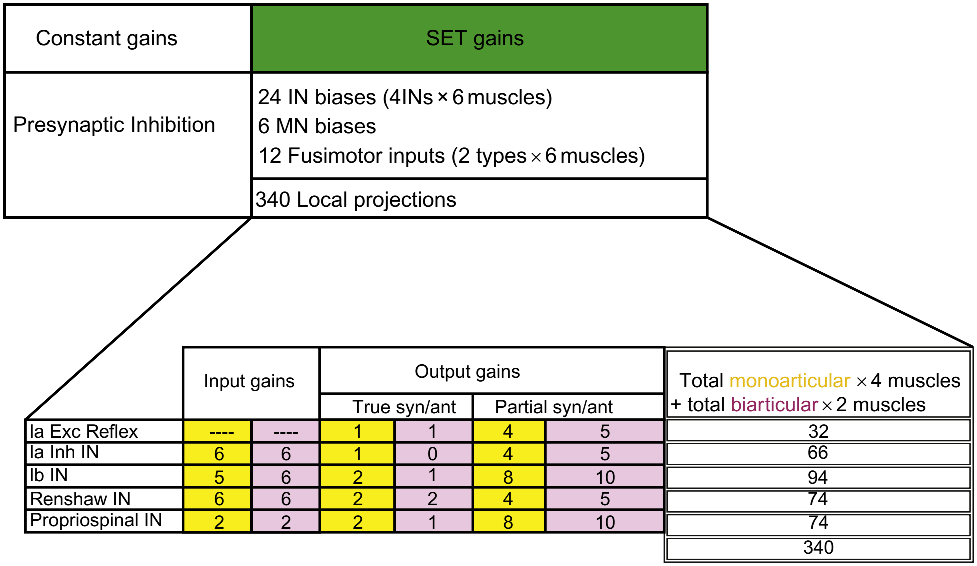
Given that the building blocks of the overall spinal network have already been defined, the major challenge in this study was to determine the functional relationships among the arm muscles to construct the network specific to this system. Although monoarticular muscles crossing a single joint are obviously antagonistic, the interaction torques among joints in the arm make it difficult to intuit the underlying muscle activity, hence whether and when a given pair of muscles acts as synergists or antagonists. Further, the system is kinetically redundant (meaning that multiple sets of muscle activation patterns can accomplish the same movement), which further complicates the relationships among the various muscles.

Kinetics and EMG studies of planar arm movement provide descriptions of muscle coordination patterns associated with reaching tasks, thus giving us insight into these functional relationships. We used the active torque analysis presented in Graham et al. (2003) to identify the functional relationships among monoarticular muscles crossing different joints. The direction of active joint torques agreed with monoarticular muscle activity from several movements presented in Karst and Hasan (1991), therefore active torque direction was a good indicator of which muscle was being recruited. We found that although reaching movements typically require that the shoulder and elbow rotate in opposite directions, the direction of active torques was often the same. In fact, all combinations of active joint torque direction between the two joints were observed, suggesting that any given pair of muscles that cross different joints act as partial synergists. EMG data from Karst and Hasan (1991) were also used to gain insight into the relationships between these muscles and the biarticular muscles, whose individual contributions cannot be deduced with confidence from net joint torques. We found that biarticular muscles could be recruited in or out of phase with the monoarticular muscles that had the same actions at the joints they crossed, suggesting that they have partial synergist relationships with the rest of the set.

In summary, each monoarticular muscle is modeled as antagonist to the monoarticular muscle crossing the same joint and partial synergist to both monoarticular muscles crossing the other joint. Each biarticular muscle is modeled as a partial synergist to all muscles in the set, including each other. The overall network consists of 340 local projections (e.g., afferent and interneuronal pathways) whose activity is modulated by the brain (see next section). The local and descending projections are distributed among 24 interneurons (four classical types for each of the six muscles) and six motoneurons whose bias is also set by the brain model (see Fig. 3).

Brain model

The brain is modeled as a task planner that evaluates performance according to criteria defined for each task and an adaptive controller



Constant gains	SET gains
Presynaptic Inhibition	24 IN biases (4INs × 6 muscles) 6 MN biases 12 Fusimotor inputs (2 types × 6 muscles)
	340 Local projections

	Input gains		Output gains				Total monoarticular × 4 muscles + total biarticular × 2 muscles
			True syn/ant		Partial syn/ant		
Ia Exc Reflex	----	----	1	1	4	5	32
Ia Inh IN	6	6	1	0	4	5	66
Ib IN	5	6	2	1	8	10	94
Renshaw IN	6	6	2	2	4	5	74
Propriospinal IN	2	2	2	1	8	10	74
							340

Fig. 3. Distribution of gains among the various interneurons and muscles. Gains are distributed into categories depending on whether they modulate the inputs or outputs of a given interneuron. Each category is subdivided further for monoarticular and biarticular muscles, as their connectivity with the rest of the muscles differs.

that adjusts its control inputs based on performance (see Loeb et al., 1999). The control inputs (normalized for the range -1 to 1) set the bias of interneurons and motoneurons (which have sigmoidal input/output functions) and the gains of the local projections within the spinal cord. The learning scheme for the adaptive controller has been described in detail in Raphael et al. (2010). Briefly, each control input is initialized at random within a relatively low range (-0.3 to 0.3) to avoid instability. The inputs are then tuned through a simple gradient descent process in which each gain is sequentially adjusted in the positive and negative direction and then left at the value that produces the best performance. One cycle through all the gains corresponds to one iteration. The model in this study was trained for three iterations and the size of the adjustments was 0.2, 0.2, and 0.1, respectively. Only three iterations were performed because they were sufficient for the model to converge on locally optimal solutions.

Modeled task

The response of a planar arm to a brief, oblique impulse (100 N × 10 ms) at the hand was simulated, equivalent to ~30 Nm extension torque at each joint. The perturbation was applied at random between 0.5 and 1.5 s into the simulation to avoid anticipation and use of momentum in the opposite direction rather than spinal reflexes to resist the perturbation. The gains of the SLR were initially set at random and adjustments were evaluated according to quadratic cost (squared deviation of the hand from the initial position integrated from 0.5 s before the perturbation to 2 s after). See Fig. 4 for a schematic overview of the task.

We also tested the response of the system when adding a modest level of cocontraction (20% activation to all muscles) to the SLR to simulate the experimental phenomenon where subjects cocontract more in the early phase of learning and to examine the effects it may have on the

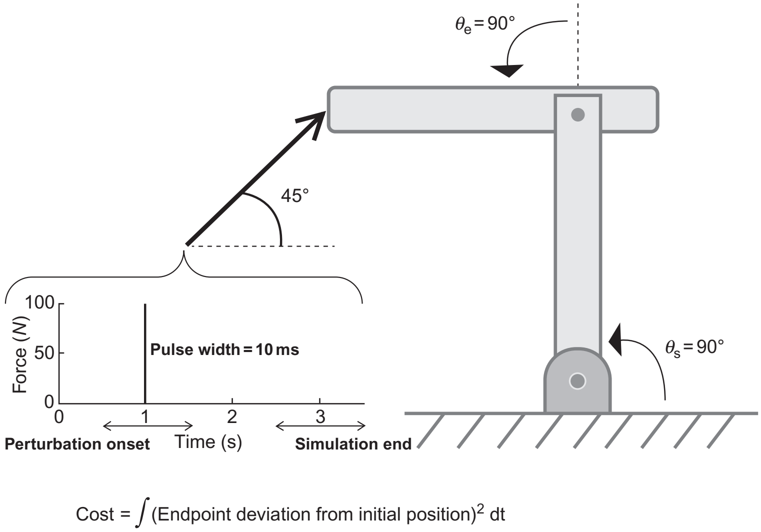


Fig. 4. Overview of the modeled task. An impulsive force (100 N × 10 ms) is applied at the end point of a stationary arm at a random onset within a 1-s interval. Task performance is measured by integrating the displacement of the arm over two and half seconds (half a second before the perturbation to two seconds after).

adaptation process. The level of cocontraction was chosen to be as low as typically adopted by experimental subjects, which itself is insufficient to stabilize the arm on its own. To gain insight into its role once performance converges, we subsequently removed the cocontraction and ran an additional training session.

Results

Training the SLR without cocontraction led to generally poor performance (mean = 0.091, SD = 0.15) that was often worse than applying cocontraction alone (SLR gains fixed at zero; Fig. 5). Most of the converged solutions were mediocre with only two being acceptable (see exemplary solutions in Fig. 5). The criteria for acceptable performance was derived from human subjects performing a similar task in Lacquaniti and Soechting (1986; although they appeared to use a much slower and smaller perturbing impulse, which was not quantified). When cocontraction was added to the SLR, the system's final performance was significantly better and less variable (mean = 0.006, SD = 0.005). All the converged solutions produced better performance than applying cocontraction alone, with over half of them being acceptable even by the strict performance criteria.

As shown in the learning curves in Fig. 5, in both cases, the initial cost did not correlate well with the cost of the converged solution. The trial with the best converged solution, for example, had one of the worst starting costs. Further, most initial starting points for the trials with cocontraction had a higher cost than those corresponding to the system being subjected to cocontraction alone. Thus, cocontraction by itself or added to a randomized SLR was not significantly better than the randomized SLR alone, but the addition of cocontraction to an SLR

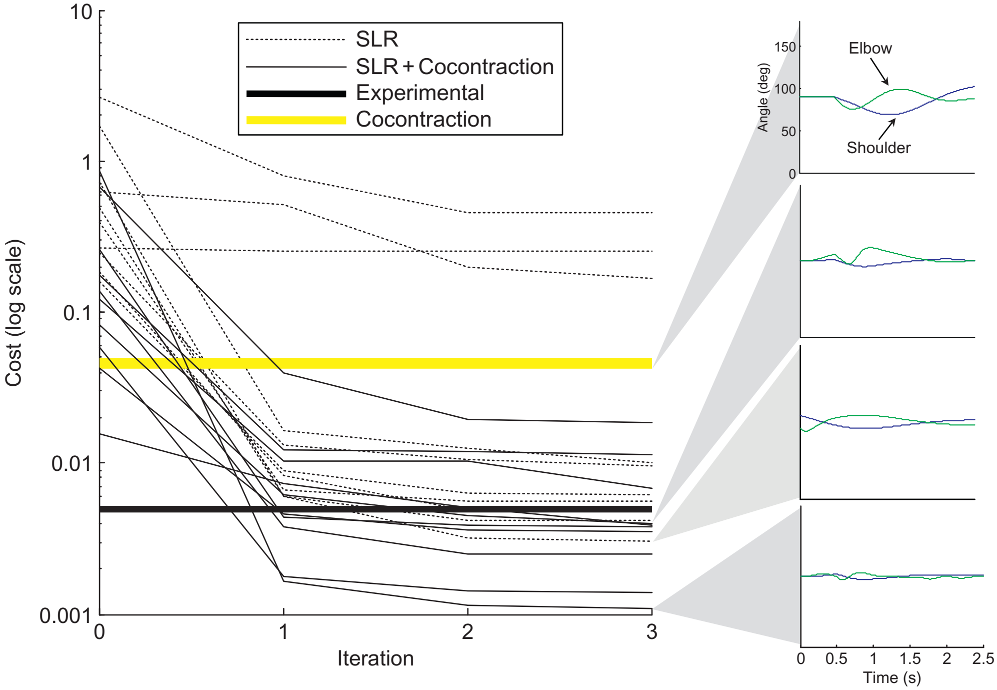


Fig. 5. Learning curves and exemplary joint angle trajectories for trials in which the spinal-like regulator was trained without (thin dotted lines) and with co-contraction (thin solid lines). The upper limit of experimental performance (derived from Lacquaniti & Soechting, 1986; thick black solid line) and modeled performance achieved when applying co-contraction alone (thick gray solid line) are also plotted for reference.

guaranteed that any randomized SLR would converge to a good performance with a modest amount of training.

Removing the cocontraction signal from a converged, well-performing system produced an immediate deterioration in performance (mean = 0.242, SD = 0.287; Fig. 6). Retraining the system using the previously converged solutions as starting points, however, achieved better performance (mean = 0.005, SD = 0.005) than the SLR responses without cocontraction. Surprisingly, they were even slightly (but not significantly) better than the SLR responses with cocontraction (SLR + cocontraction: mean = 0.006, SD = 0.005; retrained SLR following removal of cocontraction: mean = 0.005, SD = 0.005).

Discussion

Role of cocontraction in learning novel tasks

Cocontraction has been shown to be an effective strategy for stabilizing the arm in situations where external perturbations are applied (Franklin et al., 2003; Hasan, 2005; Lacquaniti and Soechting, 1986; Milner and Franklin, 2005) or a high level of accuracy is demanded (Gribble et al., 2003). Cocontraction has an obvious stabilizing effect because each muscle's viscoelastic properties, termed preflexes (see Brown and Loeb, 2000), intensifies with activation. The effects of cocontraction on learning, however, are not as intuitive because understanding them

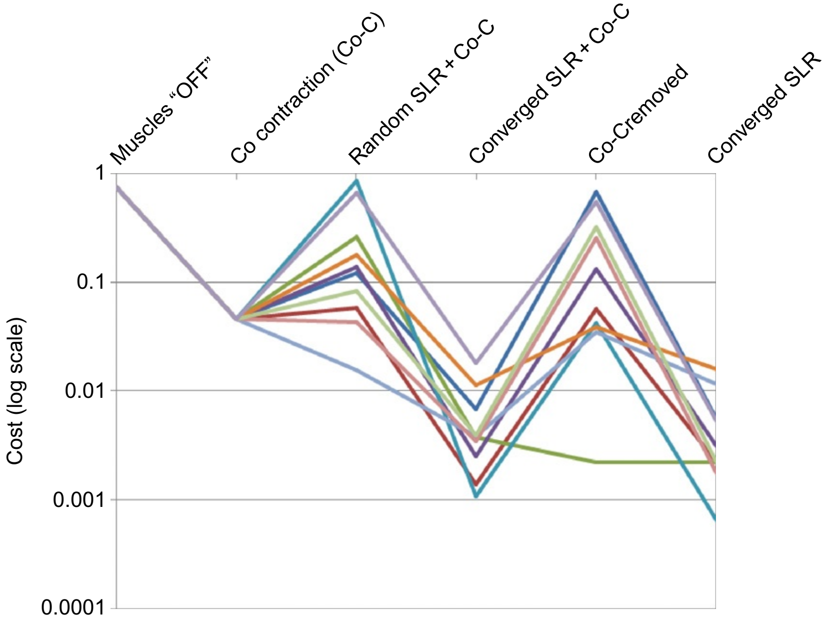


Fig. 6. Learning curves for 10 trials in which the SLR was first trained with cocontraction followed by removing the cocontraction and further training (traces from left to right). The performance achieved with inactive muscles (first point) and cocontraction alone (second point) is also shown for reference.

requires knowledge of the control points (e.g., descending inputs and reflex gains) in the sensorimotor system, their influence on the performance criteria of a given task (defined largely by the neural connectivity), and the means by which they are adjusted (i.e., type of adaptive controller). Franklin et al. (2008) show that by adjusting the degree of feedforward antagonist muscle coactivation based on position feedback, it is possible to reproduce some characteristics of physiological learning of novel tasks. This purely feedforward scheme, however, does not take into account the actual control points of the nervous system and the nature of the solution space thereby afforded. Therefore, it provides limited insight regarding the actual control problem that the nervous system encounters and the opportunity to learn to replace energetically expensive cocontraction with well-chosen gains for proprioceptive feedback.

Our results show that cocontraction reshapes the solution space, virtually eliminating the probability of entrapment in poor local minima. The local minima that are entered during learning with cocontraction are favorable starting points for learning to perform the task when cocontraction is abruptly removed. These results suggest that the tendency of subjects to resort initially to cocontraction when learning a new task (Franklin et al., 2003; Thoroughman and Shadmehr, 1999) may be an important step in the learning process that eventually results in mature strategies marked by little cocontraction and greatly decreased cortical activity.

Role of the spinal cord

The genetically specified and highly preserved connectivity of the mammalian spinal cord appears to provide a high-dimensional control space that happens to facilitate rapid and successful learning of new motor tasks. This is true even when a simplified model of the SLR is controlled by a highly oversimplified model of the brain and the algorithm by which it learns. The relatively simple and local optimization algorithm applied in this study was successful at finding many good-enough solutions because the state space defined by the SLR consists mostly of good local minima. The complex sequencing of muscle activations required to resist the perturbation in the absence of cocontraction was produced by the SLR circuitry itself acting on afferent and efference-copy signals generated by the perturbing torque and the subsequent responses of the SLR, according to well chosen but unmodulated gains preset by the controlling brain.

Limitations

The model of the brain used in this study was purposely chosen to be highly simplistic to investigate the emergent properties of the SLR. As shown in this study and in Raphael et al. (2010), the spinal cord appears to create a solution space that facilitates learning "good-enough solutions" rapidly; these are properties that are obviously useful and are presumably exploited by the brain.

The potentiality of spinal circuits may vary depending on the mechanics of the musculoskeletal system and the task. In the system described here, the added cocontraction signal (perhaps supplied by corticomotoneuronal cells in the biological system) was necessary at least initially to find good solutions with a high success rate. Interestingly, the SLR for a two degree of freedom but concentric wrist joint did NOT require any initial cocontraction to enable its controller to learn effective strategies to resist those perturbations and the solutions that it produced did not include cocontraction. It is possible that the requirement for initial cocontraction arises from the mechanical instabilities that arise in nonconcentric multiarticular systems subject to Coriolis forces.

If cocontraction is, indeed, an important feature of learning, then it would be useful for the brain itself to learn to apply and remove it according to the same learning algorithm used to adjust SLR gains. This can be accomplished by driving the learning process according to a cost function that includes both metabolic energy consumption and kinematic performance criteria. It may also be useful to employ a more biologically plausible learning algorithm in which the adaptive controller adjusts multiple SLR gains simultaneously instead of individually. These refinements of the model are currently underway and will be applied to the simple perturbation task described herein, as well as to the rich set of planar reaching tasks for which human performance data are available in the literature.

Implications for BMIs

The tasks that we have chosen to teach our model systems are similar to those that have been chosen by most researchers developing BMIs for neural prosthetic applications. It seems plausible that retraining the brain to perform tasks that it used to perform with the intact spinal cord and musculoskeletal system will be easier and more successful if the prosthetic system incorporates properties and functions similar to those being replaced or bypassed. The circuitry modeled in the SLR appears to be complex but useful. It is easily emulated in software algorithms. A subject learning to use any BMI must be trained by asking the subject to imagine performing a particular task. The recorded neural activity can then be taken as the solution to the problem of controlling the SLR. Iterative algorithms could then be used offline to find a mapping between the various BMI outputs and the available SLR inputs that successfully performs the task. We hypothesize that such a control system will generalize more readily to the wider range of tasks that subjects must learn to perform, as opposed to BMIs mapped to outputs of the musculoskeletal system.

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