

Figure 1 (Morasso & Sanguineti). Effect of the first four principal components of the motor command space. From top to bottom: tongue dorsum (arched-flat), tongue body (front-back), jaw (open-close), tongue tip (raised-lowered).

Control. From the point of view of motor control, the hypothesis about the cortical localization of the BS obviously implies a central generation of the reciprocal motor command $\vec{\Lambda}_{recipr} =$

$\vec{L}_{desired}$. The same rationale also applies to the generation of the coactivation motor command, in disagreement again with the hard-wired spinal mechanism proposed by F&L, because the geometrical complexity of learning coactivation vectors, invariant with respect to body postures, has the same nature and is of the same order of magnitude of learning the structure of M . Moreover, the grouping of muscles into antagonistic sets is not fixed but movement-dependent, thus making hypothetical spinal mechanisms much too complex. A different source of weakness of F&L's model is common to most types of equilibrium point (EP) models that rely on a sufficient stiffness level to avoid any computation of statistical/dynamical forces. The computation of such forces is indeed out of reach for any spinal mechanism and recent measures of muscle stiffness during movement (Bennet et al. 1992; Gomi et al. 1992; Tsuji et al. 1994) have revealed stiffness levels that are too low for supporting a suitable load compensation. On the contrary, in the framework of the self-organized cortical model, the knowledge about coactivation forces and static/dynamic forces can be obtained and stored in a way similar to that of the geometrical map $\vec{L} \leftarrow \vec{Q}_{func}$ outlined above. Thus, we can hypothesize that a complementary part of the BS is a set of force maps $\vec{F} \leftarrow \vec{Q}_{func}$, which associate required force vectors to each desired postural configuration.⁴ However, such a scheme does not rule out the (restricted form of the) λ model, represented by Equation (1).

We hypothesize a spinal circuitry capable of inverting the functional characteristic (1):

$$\lambda = l - \alpha^{-1}(f) \tag{2}$$

as the final step of the motor planning and control process. In this view, the central part of the process consists of binding together the different cortical maps (in a way that can be dependent on specific task-constraints, attentional aspects, etc.) and the peripheral part has the purpose of processing in parallel the outflow of coordinated positional and force vectors ($\vec{L}_{desired} = \vec{L}_{desired}(t)$ and $\vec{F}_{expected} = \vec{F}_{expected}(t)$)⁵ at the site of each muscular actuator by means of spinal circuits that implement the local inversion rule (2), thus computing the CV of each muscle.

NOTES

1. A specific form of the IC, consistent with the experimental data shown in the target article, is the following one: $\alpha(x) = \rho R(e^{x\mu} - 1)$, where μ is a universal parameter characteristic of muscle tissues, ρ is a parameter proportional to the strength of the muscle, and $R()$ is a unit-ramp function.
2. The sequence of X-ray images of the vocal tract was acquired at the Institut de Phonétique of the University of Strasbourg during normal speech and made available to our lab in the framework of the Esprit Basic Research project *Speech-Maps*.
3. The first 4 components explain more than 86% of the variance (93% for the first 6 components). The PCA can only estimate a linear approximation of M .
4. The existence of different cortical areas with similar somatotopic organization but different sensitivity to loads and force levels accords with this view.
5. Note that $l_{desired} = \lambda_{reciprocal}$. The essential difference from the standard EP models is that f is not limited to coactivation but also takes into account load compensation.

Command invariants and the frame of reference for human movement

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Abstract: We describe a solution to the redundancy problem related to that proposed in Feldman & Levin's target article. We suggest that the system may use a fixed mapping between commands organized at the level of degrees of freedom and commands to individual muscles. This proposal eliminates the need to maintain an explicit representation of musculo-skeletal geometry in planning movements.

We have recently presented a model of human jaw and hyoid motion based on the λ version of the equilibrium point hypothesis (Laboissière et al., submitted; Ostry et al. 1994). In this commentary, we review a number of features of that model and describe a solution to the redundancy problem closely related to the hypothesis of anatomical correspondence.

The model is a mathematical formulation of planar jaw and hyoid motion in which there are seven modelled muscles (or muscle groups) and four kinematic degrees of freedom. Movements are not controlled directly in terms of commands to individual muscles, but, consistent with empirical evidence (Ostry & Munhall 1994), control is organized at the level of the system's kinematic degrees of freedom. Thus, different combinations of λ s are associated with motion in each of the four degrees of freedom: jaw rotation, jaw translation, horizontal hyoid translation, and vertical hyoid translation. Cocontraction level is also controlled. These control signals may act alone or may be superimposed to produce combinations of jaw rotation, translations, and cocontraction.

We have used the model to explore the relationship between control organized at the level of degrees of freedom and control corresponding to commands to individual muscles. An important problem in this regard is whether control signals to individual muscles are adjusted to produce movements of comparable magnitude in different parts of the workspace. In effect, the question is how the nervous system takes account of musculo-skeletal geometry in planning movements.

We demonstrated, consistent with the proposal in the target article, that invariant commands could be defined associated with motion in individual degrees of freedom. We found it possible to define vector commands involving linear combinations of λ change that produced effectively independent movements in each of the model's kinematic degrees of freedom and gave essentially the same movement regardless of the starting configuration of the jaw and hyoid bone.

We observed that small but systematic errors resulted from the use of these commands because the mapping between degrees of freedom and λ s was not strictly linear. However, consistent with the suggestion in the target article, the simulation demonstrated that even in a system with complex musculoskeletal geometry, it is possible to define in the context of the λ model invariant commands associated with a simple control strategy.

The specification of invariant vector commands involved a solution to the redundancy problem that has interesting parallels to that proposed by Feldman and Levin (F&L). Because the model has seven muscles with which to define positions in a four-degree-of-freedom jaw and hyoid space, an infinite number of combinations of λ s can be associated with any stationary position of the jaw and hyoid bone. We called the set of points in λ space associated with specific jaw and hyoid positions the *no-motion manifold*. Pure commands, that is, commands for motion in individual degrees of freedom, were thus defined in terms of λ shifts between no-motion manifolds whose corresponding mechanical configurations differed only in terms of the degree of freedom in which the command was defined.

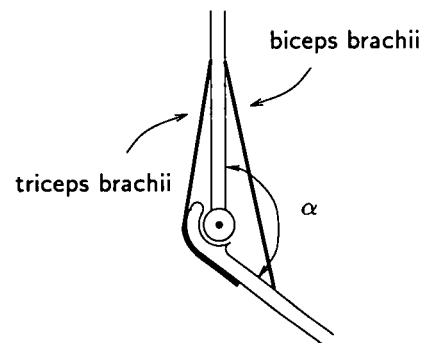
Figure 1 provides a graphical example of the technique used to solve for pure commands. The example is presented in the context of determining commands for one degree of freedom motion about the elbow. The figure shows a series of no-motion manifolds in λ space that correspond to static elbow angles ranging from 50° to 170°. The unfilled circles on each manifold represent different levels of total force, associated with different levels of centrally specified cocontraction. The filled circles indicate points of anatomical correspondence at which the cocontraction level is zero. At these points actual muscle lengths correspond to λ s and total force is zero (assuming zero gravity).

F&L suggest that, under conditions of zero cocontraction, movements may be defined by λ shifts between points of anatomical correspondence. For example, the vector labelled 1 in Figure 1

corresponds to the command for a shift from 90° to 110°. In the jaw model, we arrive at a related though different solution. Because we wished to test the plausibility of the idea that the motor system might use an invariant mapping between joint angular change and λ change, we sought commands that would work equally well in all parts of the workspace. We suggested that the direction of the invariant command in λ space might correspond to the population mean for λ shifts between adjacent no-motion manifolds. Specifically, we determined the direction of the vectors from one manifold to the next by finding for each of a number of points on an initial no-motion manifold the shortest vector to a linear approximation of the adjacent manifold. By repeating this procedure throughout the workspace we were able to obtain a population mean that we have used as the invariant command. In the arm model shown in Figure 1, the direction of the control vector obtained in this way is labelled 2.

In the jaw model, the process of determining the shortest vectors involves sampling positions along an initial no-motion

SIMPLIFIED ELBOW MODEL GEOMETRY



NO MOTION MANIFOLDS AND INVARIANT COMMANDS

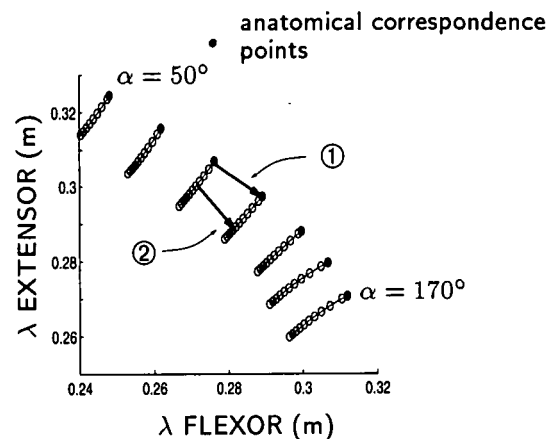


Figure 1 (Ostry et al.). Simplified elbow model geometry (top panel); no motion manifolds and invariant commands (lower panel). In computing the no-motion manifolds, the muscle moment arm of triceps brachii was assumed to be constant; the biceps brachii moment arm varied with joint angle. The vector labelled 1 corresponds to a central command associated with a shift in the anatomical correspondence point. Vector 2 represents the population mean of shortest vectors between adjacent no-motion manifolds.

manifold about the point at which the sum of total force is smallest. The point is closely related to the anatomical correspondence point. However, in the jaw model the point of minimum force is different from the point of anatomical correspondence to balance gravitational force.

Both approaches give a solution to the redundancy problem by transforming control variables specified at the level of degrees of freedom to control variables for individual muscles. In the F&L formulation, movements are generated by λ shifts between anatomical correspondence points. In the example described here and in the jaw model, comparable commands are derived by taking into account a relatively wide range of total force levels. This is likely to give slightly different λ combinations in the two formulations. A desirable feature of formulation used in the jaw model is that commands do not need to be adjusted to take account of changes in musculo-skeletal geometry.

Interneurons as backseat drivers and the elusive control variable

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Abstract: It is proposed here that the spinal network of proprioceptive feedback from length and force receptors constitutes the mechanism underlying the coordination of activation thresholds for muscles acting about the same and neighboring joints. For the most part, these circuits come between motoneurons and supraspinal signals, invalidating the idea that the activation thresholds constitute control variables for the motor system.

Hypothesis of anatomical correspondence. In this hypothesis, the reciprocal command specifies the thresholds (λ values) of all muscles acting at a joint corresponding to an equilibrium position. The lengths of biarticular muscles are then specified by the R commands of the associated joints. These muscles then have an apparent threshold at one joint that is varied by motion at the other joint. Feldman and Levin (F&L) have elegantly portrayed the joint equilibrium position on a plot of thresholds at one joint versus thresholds at the other joint. The intersection of the threshold lines for both monoarticular and biarticular muscles specifies the equilibrium position for the joint. A useful feature of this graphical representation is that the ratio of the moment arms of a biarticular muscle for the two joints is related to the slope of the threshold line for that muscle. The relationships among the threshold lines can be used to predict the recruitment patterns of muscles for different configurations of the limb.

F&L go on to say that the coordination that directs the equilibrium at each joint is achieved, not by specification of all the thresholds from supraspinal sources, but rather through the action of interneuronal networks in the spinal cord that receive inputs from proprioceptive and other sensory sources. This organizational feature disqualifies λ as a control variable, because it is subject to peripheral influences. A model is then proposed that provides decoding of reciprocal and coactivation commands to an agonist-antagonist system. This model features a generalized network to mediate anatomical correspondence for this simple muscle arrangement. In addition, length and force signals are portrayed as converging onto common interneurons and therefore as having similar distributions. One would expect for the other anatomical arrangements of muscles found in the limb, however, that a network that mediates anatomical correspondence would reflect the actual architecture of the musculoskeletal system, including specialized pathways for biarticular muscles. Anatomical considerations would suggest a highly asymmetric reflex organization that is indeed found in a number of different reduced preparations, including spinal and decerebrate (Nichols 1994). In

addition, electrophysiological studies (see McCrea, 1986) as well as mechanophysiological studies (Nichols 1994) suggest that length and force pathways are distributed quite differently through a multi-segmented limb. These studies further suggest that the two kinds of feedback have different roles in mediating the correspondence between the anatomical arrangement of muscles and the thresholds of their activations, as briefly reviewed in the following paragraphs.

For the rare cases of pure, planar anatomical antagonism, reflex linkages are dominated by reciprocal inhibition, which increases the slopes of the force-length characteristics of the two muscles but does not change the thresholds in the absence of reciprocal commands. Joint stiffness is therefore increased but equilibrium point is not. For bifunctional muscles, which act about more than one axis at a given joint, movement about one axis will change the apparent threshold along the other axis. The feedback emanating from these muscles to other muscles acting at the same joint but about only one axis is force- rather than length-dependent. Negative force feedback across axes could point the force vector of muscle reaction into line with the direction of a perturbation by increasing the stiffness of the joint in that direction. This pattern suggests that force feedback influences the thresholds for muscles whose actions are partially decoupled by the multi-axis architecture of the joint.

Force feedback also links biarticular muscles across joints to monoarticular or other biarticular muscles. In these cases, the thresholds are affected by movement at the other joint and are considered to be apparent thresholds. Pathways arising from muscle spindles can also extend across more than one joint (McCrea 1986), but force-feedback pathways are generally more widely distributed among joints and across axes of rotation. Force feedback seems to be associated with muscles whose apparent thresholds can be influenced by mechanical changes elsewhere in the joint or limb, and can act to modify the thresholds of other muscles acting at the joint. Forced dorsiflexion of the ankle leads to a flexion torque at the knee by virtue of the attachments of the gastrocnemii, whereas the force feedback from the gastrocnemii to the vasti leads to an additive or compensatory change in the threshold of the vasti depending on the sign of the feedback. For negative feedback, the effect would be to reinforce the flexion action of gastrocnemius at the knee. Force feedback therefore emerges as an important coordinating influence for postural muscles (Nichols 1994) within and across joints. This coordination is achieved by altering the threshold (λ), presumably through postsynaptic inhibition or excitation. Muscles that have more flexible patterns of activation send and receive weak force feedback. Coordination of these muscles depends more on inputs from supraspinal sources or from elsewhere in the spinal cord.

Status of the lambda model. An attractive feature of the lambda model as originally formulated by Feldman lay in part in the notion that λ , the threshold for a given muscle, could be a control variable. However, the fact that the inputs to a motoneuron pool receive contributions from peripheral as well as central sources by way of interneuronal convergence invalidates this idea. Even the possibility that a change in λ caused by internal signals could be a control variable is in question. It is conceivable that the threshold for a given muscle might not change at all for some changes in a central signal. There would therefore be a nonunique relationship between threshold and control variable. The Equilibrium Point Hypothesis is a powerful model of neuronal integration, but the meaning of λ itself has changed. One of the challenges for research indicated by F&L is to understand the mechanisms underlying recruitment across motoneuron pools. Given the broad success of the Size Principle (Cope & Clark, in press), the organization of motor unit recruitment across muscles can be understood if the thresholds and recruitment gains for each muscle or motor pool are known.

A better analogy for the aliens' experiments would be as follows.