Cerebral Control of Speech and Limb Movements G.E. Hammond (editor) © Elsevier Science Publishers B.V. (North-Holland), 1990

## Chapter 2

# CONTROL OF HUMAN JAW AND MULTI-JOINT ARM MOVEMENTS

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We present models based on the equilibrium point (EP) hypothesis for planar human jaw and arm movements. According to this hypothesis, central commands control the EP of the system by setting motoneuron recruitment thresholds ( $\lambda s$ ). In multiple muscle systems, these commands control-the  $\lambda s$  of many muscles in concert. We posit basic central commands which control specific motor functions via various combinations of  $\lambda s$ . One command is associated with the level of co-activation of all muscles and other commands are associated with motions in specific degrees of freedom. Both models include two degrees of freedom either distributed across joints (arm) or located at a single joint (jaw). We suggest that arm motions are planned in equilibrium coordinates corresponding to the position of the hand in space whereas jaw motions are planned in equilibrium coordinates associated with rotation and translation of the jaw. In both cases, we argue that the nervous system need only specify the direction and rate of change of the EP (i.e., equilibrium velocity vector). In

the absence of special constraints, we propose that the EP is simply shifted at a constant velocity. We show that the models can account for experimental kinematic and electromyographic records in speech, mastication, and reaching movements.

# Introduction

In this chapter, we examine the organization of human multi-joint arm movements in reaching and motions of the mandible in speech and mastication. The control of these limb and orofacial behaviors is explored within the framework of the equilibrium point (EP) hypothesis (Feldman, 1986). This hypothesis suggests that voluntary movements arise as a consequence of shifts in the equilibrium state of the motor system. The equilibrium state is determined by the dynamic interaction of central control signals, spinal reflex mechanisms, muscle properties, and external loads. Central command signals control this process through the specification of motoneuron (MN) recruitment thresholds and thus are able to produce desired movements and postures. We present a vectorial representation of central commands (*command vectors*) which is especially convenient for modeling multi-muscle systems.

The EP hypothesis posits a common mechanism - the central parameterization of MN recruitment thresholds - underlying the control of unrestrained free motions (e.g., reaching) and compliant or restricted motions involving contact forces (e.g., mastication). The hypothesis can also be generalized to different articulatory systems including those involved in multi-joint arm movements, orofacial movements, and eye movements (Feldman, 1981). Thus, the EP hypothesis provides a vehicle through which the underlying control of these systems can be compared.

In this paper, mathematical models are used to examine and compare multi-joint human arm movements and jaw motions. The two models are applications of the EP hypothesis to motor systems with multiple degrees of freedom either distributed to different joints (the arm) or associated with one joint (the jaw). These models, which have been implemented in computer simulations, are used to explore the form of central control signals underlying the generation of trajectories (i.e., time sequences of positions and/or forces). Simulated trajectories, based on hypothetical central commands, are compared with experimental kinematic records. In addition, electromyographic (EMG) patterns predicted by the models are examined for different movements.

The EP hypothesis offers a fundamentally different view of motor control from what can be called the computational approach. According to the latter, motion trajectories are pre-planned by the nervous system which then *solves* the inverse-dynamics equations in order to determine the torques required to achieve the planned trajectory (see Hollerbach, 1985, for a discussion of this approach). In contrast, the EP hypothesis suggests that muscle activations and forces arise as a natural dynamic reaction to differences between the actual position of the system and its equilibrium position specified by central control signals.

The EP models described in this chapter are based on the  $\lambda$  model developed by Feldman and his colleagues (see Feldman, 1986, for a review) rather than the  $\alpha$  model advocated by Bizzi and his co-workers (e.g., Bizzi, Accornero, Chapple, & Hogan, 1984). According to the  $\alpha$  model, the central nervous system controls muscle activation, and consequently muscle stiffness, in order to shift equilibrium. Thus, the  $\alpha$  model cannot explain how the motor system specifies the position of isoelectric loads which require a constant level of muscle activation regardless of position. Similarly, force control models cannot explain how the system specifies the position of isotonic loads which require a constant level of force regardless of position. The difficulty with the  $\alpha$  model is that changes in muscle activation are considered as a cause of shifts in equilibrium. In the  $\lambda$ model, the causal sequence of events during movement production is quite different: another variable (recruitment threshold or  $\lambda$ ) underlies shifts in the equilibrium whereas muscle activations are an effect of this process. Thus, the model offers an alternative to the traditional view that muscle activation is the prime reason underlying movement production.

Through their influence on the MN recruitment thresholds ( $\lambda$ s) of muscles, central commands control specific motor functions. One command is associated with the level of muscle co-contraction and other commands correspond to motion associated with specific degrees of freedom. In the arm model, in addition to a co-contraction command, there are separate commands for motions about the shoulder and elbow. Likewise, in the jaw model there are commands for rotation and translation of the mandible as well as the command for co-contraction. In general, in multiple muscle systems, central commands act on the  $\lambda$ s of several (or all) muscles. For example, in the jaw model, the  $\lambda$ s of all three modeled muscles (closer, opener, and protruder) must be controlled in concert in order to rotate or translate the mandible or to produce co-activation without motion.

Physiologically, the parameter  $\lambda$  is associated with the threshold of MN recruitment. This corresponds, in biomechanical terms, to an invariant force-length (or torque-angle) characteristic (Feldman, 1966). Consequently, positional degrees of freedom associated with central commands are naturally transformed into force degrees of freedom. By specifying  $\lambda$ s, the central nervous system can control both position as well

as force involved in compliant or restricted motion including isometric conditions.

Recent studies of multi-joint arm pointing movements have focused on the issue of planning coordinates. On the basis of kinematic variables, researchers have debated whether these movements are planned in terms of hand coordinates or in terms of joint coordinates. Straight line hand paths and invariant bell-shaped hand speed profiles have been taken as evidence of hand planning (Abend, Bizzi, & Morasso, 1982; Flash & Hogan, 1985) whereas similarities in joint angular velocity profiles have been taken as evidence of joint planning (Hollerbach & Atkeson, 1988; Soechting & Lacquaniti, 1981). These studies assume that kinematics give a reliable measure of the central control signals underlying trajectory formation. However, the EP hypothesis views kinematics as a consequence of shifts in the equilibrium position of the system. Depending on movement dynamics, actual trajectories may deviate substantially from the underlying equilibrium trajectories (i.e., time sequences of equilibrium positions). Thus, according to the EP hypothesis, the issue of planning coordinates should focus on equilibrium trajectories rather than actual trajectories. Since the former cannot be directly measured, models are required so that simulated movements, based on hypothetical equilibrium trajectories, can be compared with empirical records.

We assume that trajectories are planned in neural control or equilibrium spaces which map onto external physical spaces. Specifically, it is suggested that multi-joint reaching movements are generally planned in terms of the equilibrium position of the arm endpoint (equilibrium hand coordinates). During movement execution, these coordinates are transformed into equilibrium joint coordinates. However, some movements may be planned directly in equilibrium *joint* coordinates thereby bypassing the equilibrium *hand* planning level. It is also suggested that jaw motions are planned in equilibrium spaces corresponding to rotation of the mandible about the temporo-mandibular joint (TMJ) and translation of the centre of rotation of the mandible (i.e., the mandibular condyle) along the articular eminence. Evidence from jaw movement in speech indicates the independence of rotation and translation (see below).

In this chapter, we argue that regardless of the particular equilibrium coordinates in which movements are planned, the nervous system need only plan the rate and the direction of the shift in the equilibrium position (i.e., the nervous system specifies an equilibrium velocity vector). However, information concerning movement amplitude is not required in order to plan or initiate a movement. Note that amplitude depends on both the speed and the duration of the shift. The latter may be planned prior to movement onset or determined during the movement. In contrast, Flash (1987) has suggested that human point-to-point arm movements are characterized by equilibrium velocity profiles which are bell-shaped and scale with both amplitude and duration. Consequently, amplitude must be specified during initial planning in order to scale the equilibrium trajectory appropriately.

In summary, the EP hypothesis provides a common departure point for the examination of the control of multi-joint reaching movements and jaw movements in speech and mastication. Computer simulations, based on the EP hypothesis, are used to explore the form of central control signals underlying the production of these behaviors. Although orofacial and multi-joint limb movements may be planned in different neural control spaces (or equilibrium coordinates), we suggest that essential features of the control signals are equivalent. Specifically, we argue that the central nervous system selects an equilibrium velocity vector which specifies the direction and rate of shift of the equilibrium state of the system.

## The $\lambda$ Model

In this section, we present a mathematical treatment of the  $\lambda$  model. Where relevant, differences between the multi-joint arm model and the jaw model will be emphasized. For further information concerning the mathematics of the  $\lambda$  model, see Feldman (1980), Feldman (1986), and Feldman, Adamovich, Ostry, and Flanagan (1990).

Figure 1 presents schematics of the two-joint planar arm model (1A) and the two degree of freedom planar jaw model (1B). The arm model has six muscles including single-joint antagonists at the shoulder and elbow and double-joint antagonists. Three muscles are represented in the jaw model: jaw closer, jaw opener, and jaw protruder. In the arm model, there is a single degree of freedom associated with each joint. In the jaw model, there are also two degrees of freedom which correspond to translation of the condyle along the articular eminence and rotation of the mandible about the condyle.

## **Muscle Activation**

The  $\lambda$  model suggests that central commands are associated with changes in MN membrane potential. Specifically, central commands parameterize the threshold length ( $\lambda$ ) of MN recruitment which may correspond to the threshold of the tonic stretch reflex. Under static conditions, when muscle length (x) exceeds  $\lambda$ , MNs are recruited and the muscle will be active. Consequently, the condition of muscle activation is x >  $\lambda$ . It follows that muscles can be activated either by stretching the muscle or by shifting  $\lambda$  via central commands.

#### MODEL BIOMECHANICS







TWO DEGREE-OF-FREEDOM JAW MODEL





Figure 1. Schematics of the two-joint planar arm model (A) and two-degree of freedom planar jaw model (B). The arm model comprises three antagonistic muscle pairs including double-joint muscles. The jaw model includes a protruder muscle as well as closer and opener muscles which also act as retractors.  $\Theta_1$  and  $\Theta_2$  are the shoulder and elbow joint angles (A) and  $\alpha$  and  $\tau$  are jaw rotation and translation (B). To find the dynamics of jaw motion, the jaw was modeled as a pendulum with a point mass, m, located at length 1. The pendulum is free to rotate,  $\alpha$ , about a moving suspension point,  $\tau$ , which is itself free to translate (C). For simplicity, the level of MN recruitment (A) is assumed to increase linearly with the difference between the actual muscle length and the threshold length such that  $A = x - \lambda$ . Under dynamic conditions (i.e., during motion) muscle activity also depends on the rate of change of muscle length (x'). Activity increases with the rate of muscle lengthening and decreases with the rate of shortening. Thus, muscle activity in dynamics is:

$$A = x - \lambda^* \tag{1}$$

where  $\lambda^* = \lambda - \mu \cdot x'$  is the dynamic threshold length and  $\mu$  is the coefficient of reflex damping due to homonymous muscle spindle afferents. In the present models,  $\mu$  is assumed to be constant. However, this parameter may be under central control via gamma dynamic and beta MNs.

#### Muscle lengths and threshold lengths

In the arm model, we have made the simplifying assumptions that muscle moment arms  $(a_i)$  are constant and that muscle length varies linearly with joint angle(s). However, it should be noted that the moment arms of the elbow flexors (i.e., biceps brachii, brachialis and brachioradialis) vary by a factor of approximately two over the working range of the joint (An, Hui, Morrey, Linscheid, & Chao, 1982; van Zuylen, van Velzen, & Denier van der Gon, 1988). Although position-dependent moment arms will be included in future versions of the arm model, this will not alter its essential characteristics.

In general, the actual and threshold lengths of the muscle can be represented as angles:

$$\Theta_{i} = (x_{i} - b_{i})/a_{i}$$
(2)  
$$\underline{\lambda}_{i} = (\lambda_{i} - b_{i})/a_{i}$$

where  $b_i$  is a constant length which is independent of the actual joint angle  $(\Theta_i)$  and  $\underline{\lambda}_i$  is the threshold angle. In the special case of the double-joint arm muscles (e.g., biceps and triceps), muscle length  $(x_3)$  depends on both the shoulder angle  $(\Theta_1)$  and the elbow angle  $(\Theta_2)$ . Therefore, we define a joint angle  $(\Theta_3)$  and a threshold angle  $(\underline{\lambda}_3)$  as follows:

$$\Theta_3 = (x_3 - b_3)/(a_1 + a_2)$$
(3)  
$$\lambda_3 = (\lambda_3 - b_3)/(a_1 + a_2)$$

where  $a_1$  and  $a_2$  are the moment arms at the elbow and shoulder respectively and  $x_3 = a_1 \cdot \Theta_1 + a_2 \cdot \Theta_2 + b_3$ . Note that  $\Theta_3$  defines a family of joint configurations (i.e., arm postures) subject to the kinematic constraint described in Equation 3. The transformation between linear and angular variables (Equations 2 & 3) has the same form for both muscle and threshold lengths.

In the jaw model, actual and threshold muscle lengths are based on an explicit representation of the geometry of the jaw system (see Figure 1B). Consequently, unlike the arm model, muscle length is a non-linear function of position (i.e., mandible rotation and translation).

#### **Reciprocal Inhibition**

Reciprocal inhibition of antagonist muscles mediated through Ia interneurons (INs) has been included in the multi-joint arm model. Ia INs receive effective inhibitory inputs from Renshaw cells (Hultborn, 1972). In addition, the Ia spindle afferents of agonists produce excitation of the Ia INs which inhibit the MNs of the antagonist muscles. Ia INs are also influenced by descending pathways (Grillner, 1981; Lundberg, 1975). Reciprocal inhibition (RI) has not been included in the mandibular model since Ia INs have not been found in the orofacial system (see Luschei & Goldberg, 1981).

Feldman & Orlovsky (1972) have shown that the threshold of the stretch reflex of the gastrocnemius muscle in the decerebrate cat increases when the antagonist is stretched. Thus, we suggest that the dynamic threshold length  $(\lambda^*)$  modified by RI can be represented as the summation of the dynamic threshold length  $(\lambda^*)$  defined in Equation 1 and a value  $(\lambda^*_s)$  associated with antagonist spindle activity:

$$\lambda^{*} = \lambda^* + \lambda^*_{S} \tag{4}$$

When the muscle is stretched, the antagonist muscle is shortened and the magnitude of the inhibitory effect  $(\lambda_s)$  decreases. Thus, muscle activity,  $A = (x - \lambda^*)$ , increases more than it would in the absence of RI. Consequently, the effect of RI is to increase the magnitude of the muscle stiffness (in both agonists and antagonists) which also increases joint stiffness. RI also decreases the co-contraction area (in which both the agonist and antagonist are active) since both the threshold lengths of both the agonist and antagonist muscles are lengthened. The dependence of  $\lambda_s^*$  on antagonist muscle spindle activity can be controlled in different ways by central commands and has been described in detail (Feldman et al., 1990).

#### **Muscle Forces and External Loads**

An increase in muscle activation is associated with recruitment of MNs and an increase in their firing. As a result, both the muscle force and stiffness increase. To a first approximation, we assume that the stiffness increases linearly with A. Thus, muscle force (F) increases as a parabolic function of A:

$$\mathbf{F} = (\mathbf{k}_{0} + \mathbf{k}' \cdot \mathbf{A}) \cdot \mathbf{A}$$
(5)

where  $k_0$  is the initial muscle stiffness (when  $x = \lambda^*$ ) and k' is the rate of change of stiffness with changes in A.

The form of Equation 5 defines an invariant characteristic (Feldman, 1966) which represents the force-length properties of the muscle together with afferent feedback. Both muscle activity (A) and muscle force (F) are velocity-dependent. Equation 5 must be considered as a simplification of the relationship between force and muscle activity which doesn't take into account either Hill's force-velocity relation or muscle fiber force decay properties.

In the two-joint arm model we have assumed that the moment arms and rates of change of stiffness (k') of antagonist pairs acting about a joint are equivalent. The moment arms of the single-joint muscles are assumed to be 3 cm and the moment arms of the double-joint muscles at the shoulder and elbow are assumed to be 1 cm and 3 cm respectively. The ratio of k' of the single-joint shoulder muscles to the single-joint elbow muscles is assumed to be 2:1 and the ratio of k' for the single-joint elbow muscles to the double-joint muscles is assumed to be 1:1.

In the jaw model, the ratio of k' of the jaw opener to the jaw closer is assumed to be 1:4 and the ratio of the jaw opener to the jaw protruder is assumed to be 1:2. The moment arms of the openers and closers are computed from a geometric model (see Figure 1B) and depend on the position of the mandible.

In the computer simulations, it is necessary to compute the kinematic consequences of the torques and forces acting on the limb or mandible. For the arm model, the Newton-Euler equations of motion are used (e.g., Hollerbach & Flash, 1982). To find the equations of motion for the jaw model, the mandible was represented as a moving pendulum with a point mass (m) located at length l (see Figure 1C). The pendulum is free to rotate ( $\alpha$ ) about a suspension point which is itself free to translate ( $\tau$ ) diagonally (at angle  $\beta$ ). From the Lagrangian, a generalized torque ( $Q_{\alpha}$ ) and a generalized force ( $Q_{\tau}$ ) can be obtained:

$$Q_{\alpha} = \mathbf{m} \cdot \mathbf{l} \cdot \tau'' \cdot \cos(\alpha + \beta) + \mathbf{m} \cdot \mathbf{l}^2 \cdot \alpha'' + \mathbf{m} \cdot \mathbf{g} \cdot \mathbf{l} \cdot \sin(\alpha)$$
(6)  
$$Q_{\tau} = \mathbf{m} \cdot \tau'' + \mathbf{m} \cdot \mathbf{l} \cdot (\alpha \cdot \cos(\alpha + \beta) - \alpha'^2 \cdot \sin(\alpha + \beta)) - \mathbf{m} \cdot \mathbf{g} \cdot \sin(\beta)$$

It should be noted that rotation torque  $(Q_{\alpha})$  produces translation ( $\tau$ ) and that translation force  $(Q_{\tau})$  produces rotation ( $\alpha$ ). Q $\alpha$  is the sum of muscle,

gravitational, and contact (e.g., bolus) torques about the condyle and  $Q_{\tau}$  is the sum of the corresponding forces projected along the articular eminence.

To examine mastication movements with the jaw model, we included a simulated bolus and placed kinematic constraints on the motion of the mandible at occlusion. The width, compliance, and location of the bolus relative to the mandible can be specified (see Figure 1B). For simplicity, we assumed a bolus with linear stiffness such that force increased monotonically with compression. At occlusion (i.e., when any point on the mandible contacts the occlusal plane), neither rotation nor translation of the jaw is permitted. Once the jaw is in occlusion, it remains motionless until the force normal to the occlusal plane produces opening. In the model, the occlusal plane was assumed to be horizontal. Thus, the normal force at contact is equal to the sum of the vertical projections of muscle, gravitational, and bolus forces in addition to the vertical projection of the reaction force acting at the condyle perpendicular to the articular eminence. Although we have only examined restricted or compliant motion in the jaw model, the arm model can also be used to investigate motions such as grasping, drawing, and other behaviors involving external contact forces at the movement endpoint.

### **Central Commands: Vector Representation**

In this section, we develop a vector representation of central commands which is especially convenient for modeling multi-muscle systems. The basic ideas are illustrated by considering a single-joint system and then extended to the modeling of mandibular and multi-joint arm motions.

#### Single degree of freedom

Consider a single joint with two antagonist muscles which can be controlled by two parameters,  $\lambda_1$  and  $\lambda_2$ , which specify the MN recruitment thresholds ( $\lambda$ s) of the flexor and extensor respectively. We define two functionally different commands which control the  $\lambda$ s of antagonist muscle pairs as a single unit. The co-contraction command,  $\Lambda_{c'}$  gives rise to an increase in the activity of antagonist muscles (and therefore stiffness) while the joint remains motionless. The other command,  $\Lambda_{\Theta}$ , shifts the equilibrium position of the joint and is associated with reciprocal changes in flexor and extensor activity. Both commands thus produce simultaneous changes in  $\lambda$ s but they do so in different ways. Figure 2A shows these commands represented by vectors in the space of  $\lambda_1$  versus  $\lambda_2$ . This space has orthogonal basis vectors  $\mathbf{e_1}$  and  $\mathbf{e_2}$  (vectors are bold-faced in this paper). The projections of vector  $\Lambda_c$  have the same sign and thus the  $\Lambda_c$  command produces changes of  $\lambda$ s in the same direction. In contrast, the

projections of vector  $\Lambda_{\Theta}$  have opposite signs and consequently the  $\Lambda_{\Theta}$  command produces changes of  $\lambda$ s in different directions. The vector commands can be graded in magnitude to produce commands of varying strength. The vector commands are orthogonal and the corresponding functions can be controlled independently. Any voluntary movement control vector can be represented as a linear sum of these two basic command vectors (the principle of superposition). Unit activity recordings from motor cortex in monkeys support a distinction between central coactivation commands and movement related commands associated with reciprocal changes in muscle activity (Humphrey & Reed, 1983).

These basic command vectors can be expressed in terms of threshold angles ( $\underline{\lambda}$ s) as shown in Figure 2B. Figures 2C and 2D illustrate the effects of the command vectors in terms of shifts of invariant torque-angle characteristics (thick curves) of the flexors and extensors and changes in joint stiffness associated with the slope of the net torque-angle relationship of the joint (diagonal lines). The co-contraction command ( $\Lambda_c$ ) shifts the two characteristics in opposite directions (2C). As a result, muscle torques and joint stiffness increase but the equilibrium position remains unchanged. (The equilibrium position under static conditions is the point at which the net joint torque is zero.) The reciprocal command ( $\Lambda_{\Theta}$ ) shifts the two characteristics in the same direction (2D). Consequently, the equilibrium position changes but the level of co-activation and joint stiffness in the new equilibrium position remains the same.

The two vector commands can be presented in the following general form:

$$\Lambda_{\mathbf{c}} = \mathbf{c} \cdot (\mathbf{p}_1 \cdot \mathbf{e}_1 + \mathbf{p}_2 \cdot \mathbf{e}_2) \tag{7}$$
$$\Lambda_{\Theta} = \mathbf{r} \cdot (\mathbf{q}_1 \cdot \mathbf{e}_1 + \mathbf{q}_2 \cdot \mathbf{e}_2)$$

where c and r are the tunable strengths of the commands and  $p_i$  and  $q_i$  are the coordinates of the constant unit vectors which indicate the directions of the commands in the  $\lambda$  space. To determine the four coordinates of the unit vectors, we take into account that their lengths are equal to 1. In addition, the unit vectors are orthogonal so that their inner product is zero. This gives us three equations with four unknowns. The fact that the  $\Lambda_c$  command does not produce shifts in the equilibrium position of the joint gives the necessary fourth relation allowing us to find numerical values of the coordinates.







Figure 2. Co-activation  $(\Lambda_c)$  and movement  $(\Lambda_{\Theta})$  command vectors for single-joint motion shown in linear  $\lambda$  coordinates (A) and angular  $\underline{\lambda}$  coordinates (B). The  $\Lambda_c$  command shifts the flexor  $(\underline{\lambda}_1)$  and extensor  $(\underline{\lambda}_2)$  threshold angles in opposite direction (C) whereas the  $\Lambda_{\Theta}$  shifts them in the same direction (D). Each  $\underline{\lambda}$  is associated with an invariant torque-angle relationship (thick curves) which summate to give the net stiffness (thin diagonal lines) about the joint equilibrium angle. Thus, the  $\Lambda_c$  command varies net stiffness without changing the equilibrium angle and the  $\Lambda_{\Theta}$  command changes the equilibrium angle without altering stiffness.

Consider this last relation in more detail. When the joint is in equilibrium, the net joint torque (Q) is zero:

$$Q = T_1 + T_2 + L = 0 \tag{8}$$

where  $T_i$  are muscle torques and L is an external load. Assume that the system is in equilibrium and a small change in the  $\Lambda_c$  command is performed. To prevent a shift in the equilibrium position, the changes in individual muscle torques elicited by changes in the  $\lambda$ s must be balanced:

$$\delta Q = \delta T_1 + \delta T_2 + \delta L = 0 \tag{9}$$

where:

$$\delta T_{i} = (\partial T_{i} / \partial \lambda_{i}) \cdot \delta \lambda_{i} = (\partial T_{i} / \partial \lambda_{i}) \cdot \delta c \cdot p_{i}$$
(10)

The partial derivatives are calculated for the equilibrium position. L does not explicitly depend on the control variables and therefore  $\delta L = 0$ . It can be shown that the following are the values of the vector coordinates:  $p_1 = 1/\sqrt{(1+s^2)}$ ,  $p_2 = s/\sqrt{(1+s^2)}$ ,  $q_1 = p_2$ , and  $q_2 = -p_1$ , where the parameter s is defined as:

$$s = - \left(\frac{\partial T_1}{\partial \lambda_1}\right) / \left(\frac{\partial T_2}{\partial \lambda_2}\right) = p_2 / p_1 \tag{11}$$

The value s = 1 corresponds to the idealized case where the anatomical arrangement and the neural regulation of the antagonist muscles are identical as has been assumed in the two-joint arm model. The deflection of s from unity characterizes the degree of the asymmetry of the system. In the jaw model, the asymmetric muscle arrangement has been taken into account.

It is clear that the nervous system does not 'compute' the necessary vector commands (or the value of s). However, we suggest that these vectors are gradually approximated through evolutionary and developmental processes according to the basic constraint that one command produces co-activation without affecting the equilibrium position whereas the other changes the equilibrium position without affecting the level of co-activation.

In general, the basis command vectors will depend on the initial equilibrium position of the system. However, in the jaw model, simulations have shown that the command vectors change negligibly across equilibrium positions. For example, the same  $\Lambda_c$  command produces co-activation without jaw movement regardless of the equilibrium position of the mandible (and the load due to gravity). This is an important result since it indicates that the central nervous system can

make use of an invariant set of basic functional control vectors independent of position and load.

A constant s parameter (Equation 11) characterizes the situation where the optimal central control vectors have been coordinated with the biomechanics of the system. We hypothesize that the neural regulation of muscle activity as well as muscle anatomy and mechanics are adjusted so that the s parameters (i.e., the basic command vectors) are invariant.

In a previous version of the  $\lambda$  model (Feldman, 1980), the cocontraction (C) command and the motion-related or reciprocal (R) command were defined in angular coordinates as:

$$C = (\underline{\lambda}_1 - \underline{\lambda}_2)/2$$
(12)  
$$R = (\underline{\lambda}_1 + \underline{\lambda}_2)/2$$

These scalar commands are related to the magnitudes of the vector commands, c and r, in Equation 7 as follows:  $R = r/\sqrt{2}$  and  $C = c/\sqrt{2}$ .

#### Two degrees of freedom: jaw motion

The vector representation of central commands can be generalized to multi-muscle systems with multiple degrees of freedom. In this section, we define the basis command vectors for the tri-muscle jaw model with two degrees of freedom. In principle, any three vectors can be combined or superimposed to generate all possible movements provided that they are not linearly dependent. However, we suggest that the three basis command vectors include a co-contraction vector  $(\Lambda_c)$  and two vectors associated with jaw rotation  $(\Lambda_{\alpha})$  and jaw translation  $(\Lambda_{\tau})$ . These commands are represented in the space  $\lambda_1$ ,  $\lambda_2$ ,  $\lambda_3$  (corresponding to the threshold lengths of the jaw closer, opener, and protruder). The  $\Lambda_c$ command affects the level of muscle co-activation without altering the equilibrium position whereas the  $\Lambda_{\alpha}$  and  $\Lambda_{\tau}$  commands produce pure rotation and translation respectively without changing the level of coactivation. The experimental records shown in Figure 4A demonstrate that the co-ordination between jaw rotation and translation can vary and that rotation and translation can be produced independently. jaw Consequently, the basic command vectors we have selected in the jaw model are consistent with experimental data.

To find the coordinates (p1, p2, p3) of the co-activation vector, we calculated two integral invariants of the system associated with the fact that the co-activation command gives neither rotation nor translation. Since, in our model, the protractor does not participate in rotation, the form of the invariant ( $s_{\alpha}$ ) associated with the rotational coordinate ( $\alpha$ ) corresponds to that defined before for single-joint movements (see Equation 11 for s):

$$\mathbf{s}_{\alpha} = -\left(\frac{\partial T_1}{\partial \lambda_1}\right) / \left(\frac{\partial T_2}{\partial \lambda_2}\right) = \mathbf{p}_2 / \mathbf{p}_1 \tag{13}$$

The second invariant  $(s_{\tau})$  is associated with the absence of translation during co-contraction. During equilibrium the translational components of the three muscle forces  $(F_{\tau i})$  and the load acting along the translation surface sum to zero:

$$Q_{\tau} = F_{\tau 1} + F_{\tau 2} + F_{\tau 3} + L_{\tau} = 0 \tag{14}$$

and so do their changes during the translational command. The second integral invariant is:

$$\mathbf{s}_{\tau} = -\left(\frac{\partial F_{\tau 1}}{\partial \lambda_1} + \mathbf{s}_{\alpha} \cdot \frac{\partial F_{\tau 2}}{\partial \lambda_2}\right) / \mathbf{s}_{\alpha} \cdot \left(\frac{\partial F_{\tau 3}}{\partial \lambda_3}\right) = \mathbf{p}_3 / \mathbf{p}_2 \quad (15)$$

In combination with the condition that  $p_1$ ,  $p_2$  and  $p_3$  are components of a unit vector, these invariants allows us to calculate the components of the co-activation vector.

To find the components of the vector  $\Lambda_{\alpha'}$  we used two constraints: the vector produces pure rotation and is orthogonal to  $\Lambda_c$ . The pure rotation constraint means that the variation of the net translation force  $(\delta Q_{\tau})$  elicited by central commands must be zero. From a theoretical point of view, the important point is that the unit vector associated with the command  $\Lambda_{\alpha}$  is unique. To find the unit vector associated with  $\Lambda_{\alpha}$  we selected, by trial and error, a voluntary vector command which produced rotation without translation. We then determined the component of this vector orthogonal to the co-activation vector ( $\Lambda_c$ ) and normalized it. (In this way, lengthy calculations were avoided.) The same approach was used to find the unit vector associated with  $\Lambda_{\tau}$ . According to the theorem formulated above, both of these vectors are unique.

The three basic control vectors in the space  $\lambda_{cl'}$ ,  $\lambda_{op'}$ ,  $\lambda_{pr}$  (corresponding to  $\lambda_1$ ,  $\lambda_2$ ,  $\lambda_3$  above) are illustrated in Figure 3A. The two motion related vector commands,  $\Lambda_{\alpha}$  and  $\Lambda_{\tau}$ , are both orthogonal to  $\Lambda_c$  but are not themselves orthogonal. However, since  $\Lambda_{\alpha}$  and  $\Lambda_{\tau}$  are not linearly dependent, they can be combined with  $\Lambda_c$  to generate any voluntary movement command. Figure 3B-E shows simulated actions of the basic control vectors. Figure 3B demonstrates that the co-activation command ( $\Lambda_c$ ) produces shifts in the three  $\lambda_s$  without motion in rotation ( $\alpha$ ) or translation ( $\tau$ ). (The extent of the changes in the  $\lambda_s$  is determined by the rate and duration of shifts in the magnitude of  $\Lambda_c$ .) The same  $\Lambda_c$  command is shown in 3C following a movement to another equilibrium position. This figure illustrates that regardless of the equilibrium position of the mandible,  $\Lambda_c$  produces co-activation without movement.



TIME (2 s)

Figure 3. Three central command vectors for the jaw model shown in  $\lambda$  space (A). The co-activation command  $\Lambda_c$  produces shifts in the three  $\lambda$ s without rotation  $\alpha$  or translation  $\tau$  (B). The same  $\Lambda_c$  command produces the same effect following a movement to another equilibrium position (C). The command produces rotation without translation (D) whereas the  $\Lambda_{\tau}$  command produces translation without rotation (E).

Figure 3D presents rotations produced by  $\Lambda_{\alpha}$  commands of varying magnitude and direction. During these rotation movements there is some translation due to dynamics (see Equation 6). However, there is no difference in  $\tau$  between the initial and final equilibrium positions. A similar pattern is shown for translation movements produced by  $\Lambda_{\tau}$  commands of varying magnitude and direction in 3E. Figures 3D and 3E show that the  $\Lambda_{\alpha}$  and  $\Lambda_{\tau}$  commands are able to produce pure rotation and translation (respectively) regardless of the extent to which they shift the system's equilibrium position in doing so. In summary, this figure shows that all three central control vectors function independently of the equilibrium state of the jaw system.

#### Two degrees of freedom: arm motion

In the two-joint arm model, we have selected three central control vectors: a co-contraction vector ( $\Lambda_c$ ) and two other vectors ( $\Lambda_{\Theta_i}$ ) associated with motion at the two joints. We chose not to specify separate  $\Lambda_c$  vectors for each joint since there is some evidence that human subjects do not control shoulder and elbow joint stiffnesses independently (Mussa-Ivaldi, Hogan, & Bizzi, 1985). As in the case of single-joint motion (see Figure 2B), these command vectors may be represented in terms of joint threshold angles ( $\lambda$ s). The  $\Lambda_r$  vector produces equal but opposite shifts in flexor and extensor  $\lambda s$  for all three antagonist muscle pairs whereas the  $\Lambda_{\Theta i}$ commands produce equal shifts in the flexor and extensor  $\lambda s$  of the two (single- and double-joint) antagonist pairs acting at the i<sup>th</sup> joint in the same direction. The three command vectors produce shifts of equal magnitude in antagonist  $\lambda s$  since the parameter s (Equation 11) of each muscle pair is unity. Unlike the jaw model, in which all three basic command vectors act on the threshold lengths ( $\lambda$ s) of all muscles, only the co-activation commands has this property in the arm model. This reflects differences in muscle geometry and in the organization of the degrees of freedom in the two systems.

We assume that goal-directed arm movements are generally planned in equilibrium coordinates corresponding to the movement endpoint rather than joint angles. In particular, we suggest that the nervous system specifies the direction and the rate of change, u(t), of the equilibrium position of the endpoint (see Figure 6). In the absence of special constraints (e.g., obstacles to be avoided or precision targets), u(t) is assumed to be constant. Consequently, the equilibrium point shifts in a straight line and at a constant velocity towards the movement target. The equilibrium position of the endpoint is then transformed into equilibrium command vectors ( $\Lambda_{\Theta i}$ ) associated with joint motion. Since the relationship between endpoint and joint coordinates is non-linear, the joint level command vectors will not, in general, be shifted at a constant rate.

# Results

In this section, simulated trajectories based on assumed equilibrium trajectories are presented and compared with actual data from multi-joint reaching movements and motions of the mandible in speech and mastication (also see Ostry & Flanagan, 1989). We will demonstrate that simple constant velocity shifts in central command vectors can account for the movement kinematic patterns in each of these behaviors.

## **Speech Movements**

The X-ray microbeam (University of Wisconsin, Madison) was used to record jaw kinematics in the mid-sagittal plane. X-ray tracking pellets were attached to the jaw (between the mandibular incisors and to both the left and right mandibular molars). Additional pellets were used to correct for planar head motion and to locate the occlusal plane. All pellet positions were projected onto the mid-sagittal plane. The jaw pellet motions were used to calculate the rotation of the condyle and the translation of its axis of rotation along the articular eminence.

Figure 4A shows a characteristic pattern of jaw rotation and translation in speech. In general, in both mastication and speech, jaw rotation ( $\alpha$ ) and jaw translation ( $\tau$ ) start and end simultaneously (see 4B) and their coordination is typically characterized by straight line paths. A number of manipulations involving both mastication and speech suggest that jaw rotation and jaw translation can be separately controlled. When jaw movements in speech were examined, the relationship between rotation and translation was not constant but varied in a systematic way with the composition of the utterance. Specifically, the slope of the relationship between translation and rotation appears to vary with the consonant (compare /sa/ with /ka/) but does not depend on the vowel or speech rate. In addition, when loud speech was compared to normal speech volumes, the jaw is translated forward but the slope of the relationship between rotation and translation is preserved (compare /sa/ loud versus fast). The co-ordination between jaw rotation and translation also varies under different mastication conditions. For example, at fast chewing rates, jaw rotation is observed without any accompanying translation whereas at slower rates, rotation and translation are coupled.



SIMULATED AND ACTUAL JAW MOTION IN SPEECH

*Figure 4.* Speech movements recorded using the X-ray microbeam are shown in A and B. The slope of the relationship between jaw rotation and jaw translation depends on consonant (/sa/ versus /ka/). The condyle is translated forward in loud as opposed to fast speech (A). Empirical records of jaw rotation and translation during repetitions of /sa/ (B). These are well accounted for by simulated motions (C) based on simple constant velocity shift in central command vectors (D).

Figure 4B shows temporal patterns of jaw rotation and jaw translation recorded during a single trial in which the subject repeated /sa/ at a loud speech volume. (This record is one of those shown in 4A). Jaw opening (decreasing  $\alpha$ ) is associated with forward translation (increasing  $\tau$ ) of the centre of the condyle. This pattern of rotation and translation is simulated in 4C. The deceleration of jaw rotation towards the end of the closing phase of the movement (see  $\gamma$  in 4C) can be attributed, in the model, to decreases in the passive muscle force associated with shortening of the jaw closer. Figure 4D shows the changes in the muscle  $\lambda$ s which produce this behavior. As shown in the figure, simple constant velocity shifts in the  $\lambda$ s can generate the smooth patterns of rotation and translation observed experimentally. The changes in  $\lambda$ s were produced by a combination of the basic command vectors  $\Lambda_{\alpha}$  and  $\Lambda_{\tau}$  with a constant level of co-activation ( $\Lambda_c$ ). Notice that the rate and duration of the  $\lambda$  shifts differ for simulated opening and closing movements.

#### **Mastication Movements**

Simulated and empirical chewing movements are illustrated in Figure 5. Three chewing cycles are shown for both the simulated movements (5A-B) and the empirical movements (5C). Each cycle consists of an initial opening phase (in which  $\alpha$  decreases and  $\tau$  increases) followed by a closing phase. Figure 5A shows simulated patterns of jaw rotation ( $\alpha$ ) and translation ( $\tau$ ) as well as simulated bite forces. During the closing movement, when the bolus is contacted, an initial bite force is developed. At the same time, the velocity of jaw rotation ( $\alpha$ ) begins to decrease. This is consistent with the empirical pattern shown in 5C (as indicated by  $\Sigma$ ). Empirically, bite force has only been measured under static conditions and consequently the simulated patterns observed with the model provide theoretical predictions to be tested experimentally.

Figure 5B shows the changes in the muscle  $\lambda$ s corresponding to the These changes were produced with a simulated motions in 5A. combination of all three basis control vectors. The level of co-activation was increased during the closing phase of the movement. During occlusion, the positional degrees of freedom of the system are transformed into force degrees of freedom. At this point, the same central control vectors can be used to control and produce forces rather than motions. As in the case of speech movements, simple constant velocity shifts in muscle  $\lambda$ s, determined by the rate and duration of shifts of the central commands vectors, can account well for the kinematic patterns observed in Note that subtle differences between cycles can be mastication. approximated by varying the delay between successive cyclical shifts in the  $\lambda$ s and their magnitude (see Figure 5B).



# SIMULATED AND ACTUAL JAW MOTION IN MASTICATION

Figure 5. Simulated jaw rotation ( $\alpha$ ), translation ( $\tau$ ) and bite force (A) based on constant velocity shift in central control vectors (B). After contact with the bolus, the jaw rotation decelerates ( $\infty$ ). Empirical records of rotation and translation are shown in C.

#### EQUILIBRIUM AND PREDICTED ARM TRAJECTORIES



HORIZONTAL ENDPOINT PATHS

*Figure 6.* Equilibrium (dotted) and 'actual' (solid) endpoint paths generated by the two-joint planar arm model (A and B). Straight line constant velocity shifts (0.9 m/s) in the equilibrium position of the endpoint result in curved paths. Corresponding equilibrium joint angles (dotted) will not shift at a constant velocity and may result in joint reversals (C). Actual joint angles (solid) may nevertheless change monotonically. Constant velocity shift in the position of the movement endpoint (1.5 m/s) can produce smooth bell-shaped tangential velocity profiles (D).

#### **Two-Joint Arm Movements**

Figures 6A-B show simulated 'actual' (solid) and equilibrium (dotted) trajectories of the movement endpoint generated with the two-joint planar arm model. Figure 6A shows a (left to right) diagonal motion whereas lateral motions in both directions are shown in 6B. The actual paths are characteristically curved (Flash & Hogan, 1985) while the paths of the equilibrium position of the endpoint form straight lines. More subtle effects such as the dependence of curvature on movement direction are also consistent with experimental data (e.g., Flash & Hogan, 1985). Figure 6C illustrates the actual (solid) and equilibrium (dotted) joint angles as a function of time corresponding to the simulated movement shown in 6A. Although the equilibrium angle at the elbow reverses direction during the motion (indicated by  $\downarrow$ ), a corresponding reversal in the actual elbow angle is not observed.

Equilibrium and actual tangential velocity profiles (corresponding to path 5 shown in 7C) are presented in Figure 6D. This figure demonstrates that the smooth bell-shaped tangential velocity profiles which have been reported for multi-joint arm movements (Atkeson & Hollerbach, 1985; Flash & Hogan, 1985) can be produced by simple constant velocity shifts in the equilibrium position of the endpoint. Thus, smoothness need not be specified at the motion planning level but may be considered as a natural consequence of the dynamics of the arm system.

Figure 7 shows shoulder EMG (7A) and kinematic patterns (7B) for the five movements shown in 7C in which the equilibrium position of the endpoint is shifted, at a constant velocity, in different directions. The magnitude and duration of the EMGs produced by the model are a function of movement direction. In the absence of joint motion reversals, the predicted agonist-antagonist EMG patterns are triphasic.

# Discussion

We have illustrated three levels of threshold length ( $\lambda$ ) regulation in our models: a *low* level associated with segmental reflex mechanisms mediated by muscle afferents, an *intermediate* level connected with basic command vectors, and a *high* level associated with the control of these basic command vectors.

The low level is associated with the tonic stretch reflex and intermuscular interactions including reciprocal inhibition (RI). The threshold of MN recruitment ( $\lambda$ ) may correspond to the threshold of the tonic stretch reflex (Feldman & Orlovsky, 1972). RI, whereby spindle afferents of the agonist muscle give rise to an increase in the threshold length of the antagonist muscle and vice versa, is associated with an

increase in total stiffness of the joint, a decrease in the level of co-activation area of the muscles, and a reduction in muscle activity in the equilibrium position without lose of stability. The tonic stretch reflex threshold and intermuscular interactions can be controlled by central commands of the intermediate level. These commands can affect the low level in different ways through their actions on  $\alpha$  and  $\gamma$  MNs, Ia INs, and Renshaw cells.

The intermediate level consists of central commands which regulate threshold lengths independently of spindle afferents. We have hypothesized the existence of a set of basic commands classified according to the functional role they play in the control of equilibrium. Each command controls the  $\lambda$ s of a set of muscles simultaneously and can be represented by a vector in  $\lambda$  space. These vectors have a constant part associated with their direction in  $\lambda$  space and a variable part representing their magnitude which is under high level control. Thus, the general form of a command vector  $\Lambda$  is as follows:

$$\Lambda = \mathbf{M} \cdot \boldsymbol{\Sigma} \, \mathbf{p}_{\mathbf{i}} \cdot \mathbf{e}_{\mathbf{i}} \tag{16}$$

where  $\Sigma p_i \cdot e_i$  is a unit vector indicating the direction of the vector  $\Lambda$ ,  $p_i$  are its coordinates,  $e_i$  are basis vectors in  $\lambda$  space, and M is the magnitude of the command vector. The variable or controlled part of the vector can be represented as:

$$M = M_{\Omega} + u(t) \cdot (t - t_{i}) \tag{17}$$

where  $M_0$  is an initial magnitude of the command vector, u(t) is the rate of its change,  $t_i$  is the time of the onset of the command, and t is time.

There are several properties of command vectors which are worth emphasizing. The rate of change, u(t), of the magnitude of a command vector and the associated onset time (t<sub>i</sub>) are under central control. In general, these parameters can differ for each command vector applied in a given movement. However, in the present chapter, we have only considered the simple case in which the onset of central commands is simultaneous. In movements without specific constraints, the rate u(t) is assumed to be constant. This assumption is supported by data on corrections in reaching and saccadic eye movements (Pélisson, Prablanc, Goodale, & Jeannerod, 1986). Pélisson et al. compared the trajectories of two movements, both directed to the same final target. In control trials only the final target was shown to the subject whereas, in 'correction' trials, the target was shifted to the final position from an intermediate position located along the path to the final target. The corrected movements coincided with non-corrected movements provided that the final target was exposed early in the movement towards the intermediate one. The same result was obtained for saccadic eye movements. This result is predicted by our model based on constant velocity control signals: to correct the movement, the control signal is simply continued (at constant velocity u) until the final equilibrium position is reached. Thus, the form of the control signal, and therefore the kinematics, will be the same for the corrected movements and the control movements.



*Figure* 7. Shoulder EMG (7A) and kinematic patterns (7B) for five movements in which the equilibrium position of the endpoint is shifted, at a constant velocity, in different directions (7C).

Another important property of command vectors is that the coordinates (p<sub>i</sub>) of a given vector are constant and can be considered as structural-functional invariants associated with a specific concordance among neuronal command structures, afferent systems, and biomechanics. For example, the invariance of the co-activation command  $(\Lambda_r)$  enables the system to produce co-activation of numerous, anatomically different muscles without motion in the joints regardless of position or external In addition to a co-activation vector, we have suggested the loads. existence of two other basic vectors associated with pure rotation and translation in jaw movements, and motion about the shoulder and elbow in the case of arm movements. Experimental records of jaw movements in speech (Figure 4A) are consistent with this suggestion but do not rule out an alternative basis vector set (e.g., associated with muscle co-activation, pure rotation, and another vector, orthogonal to the other two, associated with a combination of rotation and translation of the jaw). Vector commands can be applied in different combinations to produce different ratios of motion of each degree of freedom and co-activation.

Recent evidence on muscle synergies involved in the generation of isometric elbow torques in humans (Buchanan, Rovai, & Rymer, 1989; van Zuylen, Gielen, & Denier van der Gon, 1988) supports the notion that the activity of multiple muscles with different biomechanical functions can be controlled in concert in order to produce torques about specific degrees of freedom. Buchanan et al. (1989) have shown that when subjects produce a flexion torque at the elbow, pronator terres (a forearm pronator) activity compensates for the supination torque caused by the activation of the biceps. Thus, although the biceps both flexes and supinates the forearm, other muscles allow for the generate of pure flexion torques. (Likewise, when subjects were required to produce a forearm supination torque, triceps activity compensated for the flexion torque caused by biceps activity.)

The high level in the model of reaching movements is associated with a neuronal control or equilibrium space which maps onto the physical extrapersonal space in the sense that activation of a neuronal population localized about a point in the neuronal structure is associated with a point in the external space. In the case of multi-joint arm movements, this point coincides with the equilibrium position of the arm endpoint. It is also possible to present central commands generated at this level by goaldirected vectors which specify the rate and the direction of the shift in the equilibrium position of the endpoint to the target. This signal is then transformed into joint level commands according the scheme already described (Feldman et al., 1990). Analysis has shown that the commands which give rise to rotations of the joints are cosine functions of the angle between an optimal direction specific for each joint and the direction of the target vector. The corresponding dependence is characteristic of cortical neurons (Georgopoulos, 1988; Schwartz, Kettner, & Georgopoulos, 1988). This allows us to suggest that motor cortex neuronal activity not only reflects the direction and the magnitude of the target vector that produces shifts of the equilibrium position of the arm endpoint but also individual commands that produce shifts of the equilibrium angle for each joint.

Under certain conditions, both the rate of change, u(t), and the direction of the equilibrium vector can be modified in the course of movement. For example, u(t) may be reduced as the movement endpoint approaches the target zone in precision tasks and the direction of the vector may be altered to correct errors, react to sudden changes in the target position, or to avoid obstacles. Otherwise, if there are no specific constraints, the u(t) remains constant until the target is reached. This case has been realized in the two-joint model of reaching movements (Figures 6 and 7). Both kinematic and EMG patterns are consistent with experimental data (Flash & Hogan, 1985; Hasan & Karst, 1989).

In this chapter, we have argued that regardless of the particular equilibrium coordinates in which movements are planned, the nervous system needs only to plan the rate and the direction of the shift in the equilibrium point. Information concerning movement amplitude is not required in order to plan or initiate a movement. The amplitude of the shift in equilibrium depends on both the speed and the duration of the shift. The latter may be planned prior to movement onset or determined during the movement. In contrast, Flash (1987) has suggested that human pointto-point arm movements are characterized by equilibrium velocity profiles which are bell-shaped and scale with both amplitude and duration (i.e., u(t) is constantly varied during the movement). Consequently, amplitude must be specified during initial planning in order to appropriately scale the equilibrium trajectory.

An essential difference between Flash's (1987) model and our own concerns the role of smoothness in movement production. In the model by Flash, smoothness is considered to be a fundamental principle underlying the planning and production of movement by the nervous system (see also Hogan, 1984). In contrast, according to the  $\lambda$  model, movements are smooth because of the system's natural dynamics. In general, it is unnecessary to posit control signals which meet the maximal smoothness criterion. The  $\lambda$  model, with constant velocity shifts in the equilibrium position of the endpoint, is able to produce smooth bell-shaped tangential velocity profiles of the actual movement endpoint (see Figure 6).

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