

The control of multi-muscle systems: human jaw and hyoid movements

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Abstract. A model is presented of sagittal plane jaw and hyoid motion based on the λ model of motor control. The model, which is implemented as a computer simulation, includes central neural control signals, position- and velocity-dependent reflexes, reflex delays, and muscle properties such as the dependence of force on muscle length and velocity. The model has seven muscles (or muscle groups) attached to the jaw and hyoid as well as separate jaw and hyoid bone dynamics. According to the model, movements result from changes in neurophysiological control variables which shift the equilibrium state of the motor system. One such control variable is an independent change in the membrane potential of α -motoneurons (MNs); this variable establishes a threshold muscle length (λ) at which MN recruitment begins. Motor functions may be specified by various combinations of λ s. One combination of λ s is associated with the level of coactivation of muscles. Others are associated with motions in specific degrees of freedom. Using the model, we study the mapping between control variables specified at the level of degrees of freedom and control variables corresponding to individual muscles. We demonstrate that commands can be defined involving linear combinations of λ change which produce essentially independent movements in each of the four kinematic degrees of freedom represented in the model (jaw orientation, jaw position, vertical and horizontal hyoid position). These linear combinations are represented by vectors in λ space which may be scaled in magnitude. The vector directions are constant over the jaw/hyoid workspace and result in essentially the same motion from any workspace position. The demonstration that it is not necessary to adjust control signals to produce the same movements in different parts of the workspace supports the idea that the nervous system need not take explicit account of musculo-skeletal geometry in planning movements.

1 Introduction

In this paper, we present a model of sagittal plane human jaw and hyoid motion based on the equilibrium point hy-

pothesis of motor control (λ model). The aim is to explore how control is organized to produce movements in multiple degrees of freedom in systems that have redundant numbers of muscles and complex geometry (Bernstein 1967). We examine how muscle geometry is taken into account in motion planning and whether a command structure may be identified which may be invariant across the workspace, that is, over the full range of variation of the system's mechanical degrees of freedom. An initial version of the jaw model was described in Flanagan et al. (1990).

According to the model, movements result from changes in neurophysiological control variables which shift the equilibrium state of the motor system. One such control variable is an independent change in the membrane potential of α -motoneurons (MNs); this variable establishes a threshold muscle length (λ) at which MN recruitment begins. When the value of λ is changed, muscle activation and force increase in proportion to the difference between the threshold and actual muscle lengths. Thus, by changing λ the nervous system may produce motion to a new equilibrium position (Feldman 1986; Feldman et al. 1990).

We explore, in the context of the model, how control signals are coordinated in systems such as the jaw where muscles have multiple mechanical actions and contribute to motion in more than one degree of freedom (Buchanan et al. 1986, 1990; van Zuylen et al. 1988; Sergio and Ostry 1994). We suggest that control is not organized directly in terms of commands to individual muscles. Rather the nervous system may use a control space in which control variables are specified for each kinematic degree of freedom separately. A superposition of these basic commands produces motion in multiple degrees of freedom.

A significant problem in motor control is whether, in order to produce movements of comparable magnitudes in different parts of the workspace, the nervous system must adjust its commands to take account of muscle geometry, that is, to account for changes to the lines of muscle action. In terms of the λ model, the problem is whether it is necessary to alter the mapping between changes to joint angular commands and muscle λ s in different parts of the workspace. Our working hypothesis is that the nervous system can approximate the mapping between changes in the

control variables specified in terms of degrees of freedom and changes in the control variables at the level of muscle λ s using simple linear relationships. For each degree of freedom, the coefficients of the linear relationship may be invariant across the workspace. These invariants characterize the system's geometry. In other words, these invariants may be different for different musculo-skeletal systems such as the jaw and the arm. If such invariants do exist, it would suggest that the nervous system need not explicitly take account of musculo-skeletal geometry in planning movements.

Consider the general problem in the case of jaw movements. Jaw motions in the sagittal plane involve a combination of rotation (change in orientation) and translation (change in position). During opening, the jaw rotates downward and translates forward. The pattern is reversed during closing. Muscles such as masseter and temporalis act to raise and retract the jaw. The anterior belly of the digastric produces lowering and retraction. The lateral pterygoid produces jaw protrusion. Since there is no one-to-one mapping between muscle actions and kinematic degrees of freedom, central control signals must be coordinated to produce movements such as jaw rotation or translation, either alone or in combination.

We have previously presented empirical evidence consistent with the proposal that the nervous system organizes jaw movement in terms of an equilibrium jaw position and an equilibrium jaw orientation (Ostry and Munhall 1994). Two kinds of evidence were presented. We showed that the orientation and position of the jaw could vary separately. We also showed that when jaw orientation is plotted as a function of horizontal jaw position, the movements are characterized by straight line paths regardless of the initial orientation and position of the jaw. The evidence suggests that the system may specify jaw rotation and translation separately.

The motions of the jaw and the hyoid bone may be independent as well. In speech movements, the jaw and hyoid are both raised or both lowered for consonants, but for vowels the patterns are reversed so that for vowels such as *i* and *u* the jaw is raised and the hyoid lowered, while for vowels such as *a* the jaw is lowered and the hyoid raised (Bothorel 1975). Hyoid bone position thus may be independent of the position of the jaw.

Consistent with these empirical demonstrations we show in the work which follows that control variables at the level of degrees of freedom can be transformed into control variables for individual muscles so as to produce independent rotation and translation of the jaw, as well as independent vertical and horizontal motion of the hyoid bone (four degrees of freedom in total) and also muscle co-contraction without motion.

1.1 The Model

We provide a mathematical formulation of planar jaw and hyoid motion based on the λ model. The present version has seven modeled muscles (Table 1, Fig. 1) and four kinematic degrees of freedom. Movements in these degrees of freedom are controlled by various combinations of λ s. Specific combinations are associated with jaw rotation, jaw translation,

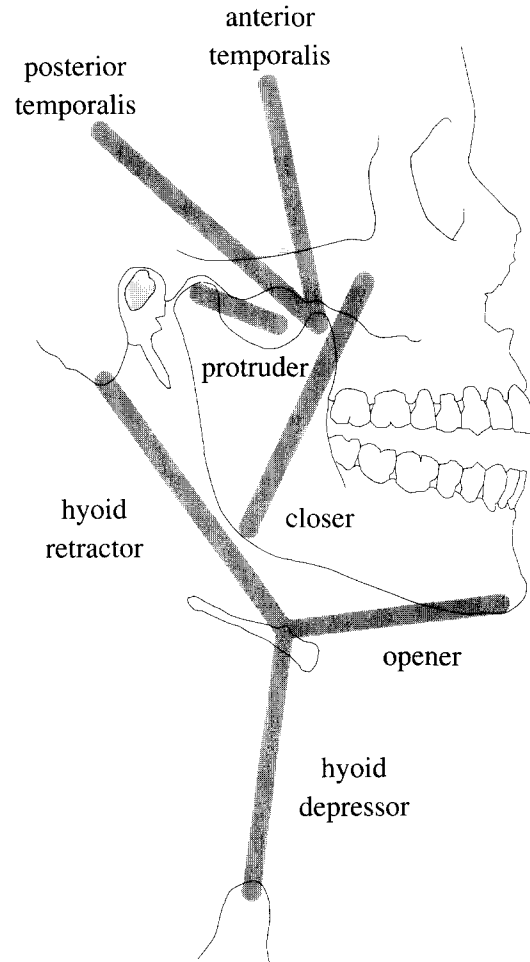


Fig. 1. Schematic representation of modeled muscles with their attachments to the jaw and hyoid bone

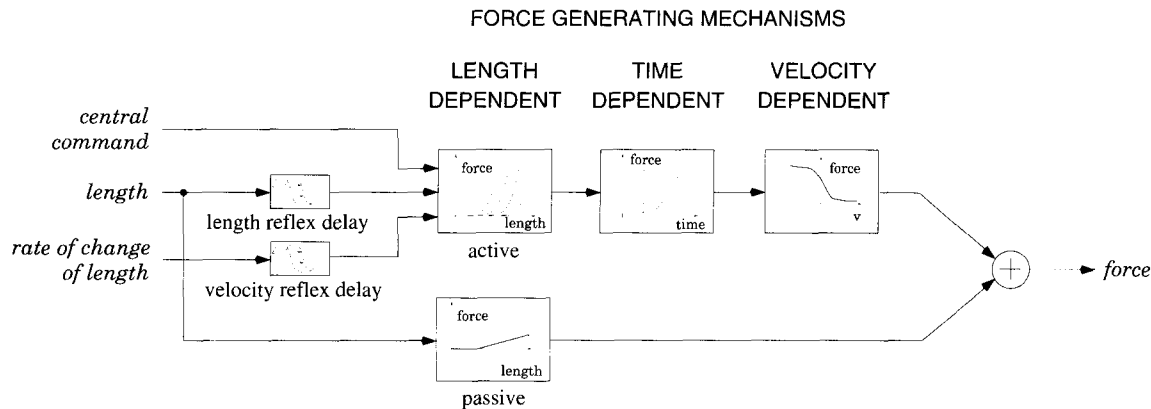
horizontal hyoid translation and vertical hyoid translation. The co-contraction level may also be controlled.

Anthropometric measurements for the model, which is shown in Fig. 1, were taken from Scheideman et al. (1980). A schematic diagram of the muscle model is shown in Fig. 2. Locations of muscle origins and insertions are based on McDevitt (1989). The present model does not include constraints due to the temporomandibular joint (TMJ) ligaments which act to limit the range of jaw motion (Baragar and Osborn 1984; Osborn 1989). In the present version of the model, we have assumed that vertical and horizontal positions of the anatomical center of rotation of the jaw are not independent [see (7)].

1.1.1 Neural control and force generation. The λ model proposes that central control signals determine threshold lengths (λ s) for α -MN recruitment by means of independent changes to MN membrane potentials [see Feldman et al. (1990) for a discussion of the relationship between threshold muscle lengths and MN membrane potentials]. Muscle activation levels (A) depend on the difference between the current muscle length (l) and λ , and the rate of muscle length change, such that activation increases with muscle lengthening rate, decreases with shortening rate and increases with deacceleration.

Table 1. Muscles represented in the model

Model muscle	Index	Real muscle
Jaw protruder	p	Inferior head of lateral pterygoid, superior head of lateral pterygoid
Jaw closer	c	Masseter, medial pterygoid
Anterior temporalis	a	Anterior temporalis
Posterior temporalis	t	Posterior temporalis
Jaw opener	o	Anterior belly of digastric, geniohyoid
Hyoid retractor	r	Posterior belly of digastric, stylohyoid
Hyoid depressor	d	Sternohyoid, thyrohyoid, sternothyroid, omohyoid

**Fig. 2.** Schematic representation of the muscle model

ing threshold. Muscle activation and force are defined as a function of the variable A , where:

$$A = [l - \lambda + \mu \dot{l}]^+ \quad (1)$$

where

$$[x]^+ = \begin{cases} x, & \text{if } x > 0 \\ 0, & \text{if } x \leq 0 \end{cases} \quad (2)$$

The parameter μ is called the damping coefficient. We would like to emphasize that, in the physiological literature, damping is associated with regulation of muscle force as a function of velocity. In contrast, the damping coefficient, μ , characterizes the dependence of the muscle's threshold length on velocity. Both proprioceptive feedback and muscle intrinsic properties are velocity dependent and thus contribute to the force-related damping in a non-linear way [see (3) and (6)]. The component of the force-related damping dependent on proprioceptive feedback is, to a first approximation, proportional to the product of muscle stiffness and the coefficient, μ (St-Onge et al. 1993). Thus, even though μ is considered, for simplicity, the same for all muscles and constant for a given movement (0.05 s), the force-related damping may still vary as a function of stiffness both for a single muscle and between muscles.

Taking into account time-varying central commands and a reflex delay of d ms, the variable $A(t)$ is defined as:

$$A(t) = [l(t-d) - \lambda(t) + \mu \dot{l}(t-d)]^+ \quad (3)$$

The reflex delay, d , is assumed to be the same for all muscles. A value of 10 ms was used for the reflex delay and was estimated from unloading responses during mastication in monkeys (Luschei and Goldberg 1981).

The model assumes that afferent input related to muscle length and velocity summate with descending input to α -MNs to give an overall level of muscle activation. In

limb muscles, position- and velocity-dependent afferent inputs arise from activity in muscle spindle receptors. In the jaw, there are many spindles in closer muscles but relatively few muscle spindles have been reported in human jaw openers. Nevertheless, the presence in jaw opening muscles of a small-amplitude tonic stretch reflex (Neilson et al. 1979) and unloading response (Lamarre and Lund 1975) both suggest that afferent input to jaw opener MNs may arise from jaw opener muscle receptors. The demonstration of a tonic vibration reflex in the human jaw (Hellsing 1977) indicates that mechanoreceptors with autogenic reflex connections may also provide this information. Reflex connections between jaw closer muscles and jaw opener MNs are another possible source of afferent input (van Willigen 1986).

Increases in muscle activation are associated with the recruitment of MNs and increases in their firing rate. The steady-state active muscle force, \bar{M} , is approximated in the present paper by an exponential function of the form:

$$\bar{M} = \rho[\exp(cA) - 1] \quad (4)$$

where c is a form parameter and ρ is a magnitude parameter related to force-generating capability and is specific to each muscle. This relationship is consistent with the size principle, where the form parameter, c , is a measure of the MN recruitment gradient. In the present paper we have assumed that c is similar for all muscles.

The parameter c was estimated from empirically obtained force-length relations for cat gastrocnemius muscle (Feldman and Orlovsky, 1972). A regression technique was used to approximate the measured force-length relations. The regression was done for the active force component with passive stiffness (which was assumed to be linear) subtracted from the total forces. The value obtained for c (0.112 mm^{-1}) is close to the range of values obtained by Feldman (1966) from torque-angle curves for the human elbow.

Table 2. Maximum muscle force and standard deviation from Pruijm et al. (1980) and estimated cross-sectional area

Muscle	Maximum Force (N)	Cross-sectional Area (cm ²)
Masseter	} 639±176	
Medial pterygoid		
Anterior temporalis	362±65	
Posterior temporalis	197±26	
Openers	115±40	2
Lateral pterygoid	378±106	
Posterior belly of digastric	} (86.3)	1
Stylohyoid		0.5
Hyoid depressors	(57.5)	1

Values in parentheses are obtained by assuming maximum force varies linearly with cross-sectional area

The magnitude parameters, ρ , for each muscle were obtained from estimates of the maximum force-generating capabilities of human jaw muscles (Prujm et al. 1980) and from estimates of muscle cross-sectional areas taken from McGrath and Mills (1984), Mills et al. (1988) and Weir and Abrahams (1978). Maximum muscle force estimates are given in Table 2. Values which were estimated on the basis of muscle cross-sectional areas are shown in parentheses. These forces were estimated on the assumption that muscle force varies linearly with the muscle's cross-sectional area.

The calcium-dependent process of excitation-contraction coupling gives rise to a gradual change in muscle force. This graded force development is generally modeled using non-linear kinetics equations [see Zahalak (1990) for a review]. In the present paper, as a first approximation, we characterize force development as a second-order, low-pass filtering of the steady-state muscle force, \tilde{M} . This filter is critically damped with a single parameter τ . A value of τ of 15 ms was chosen to give, to a step stimulus, a response which reached an asymptotic value at about 90 ms (Miller 1991). Thus, the instantaneous value of muscle force, M , gradually approaches the steady-state value, \tilde{M} . The filter is described by the following equation:

$$\tau^2 \ddot{M} + 2\tau \dot{M} + M = \tilde{M} \quad (5)$$

According to the sliding filament theory (Huxley 1957), the force generated by a muscle depends on the velocity with which the muscle is shortening or lengthening. The dependence of force on velocity was estimated from data for cat soleus muscle at different activation levels of the motor nerve (Joyce and Rack 1969). The data were fitted with a sigmoid curve that saturates for both large muscle-shortening and large muscle-lengthening velocities [see (6)]. We used an arctangent curve with four parameters as the sigmoid function. The force-velocity relation is multiplicative to the instantaneous value of muscle force, M , so that the intrinsic damping applied only to the active component of muscle force (Fig. 2). A sigmoid function was used rather than a hyperbolic, since the hyperbolic accounts for the dependence of force on velocity only in the case of muscle shortening.

Muscle force in the absence of neural input is called passive. The passive force of the muscle was assumed to vary linearly with length and to summate with active force which is generated by the recruitment of motor units. We have made the simplifying assumption that passive forces arise

Table 3. Passive muscle stiffness estimates

Model muscle	Passive stiffness (N m ⁻¹)
Jaw protruder	114
Jaw closer	192
Anterior temporalis	109
Posterior temporalis	59.4
Jaw opener	34.7
Hyoid retractor	23.1
Hyoid depressor	17.3

only for muscle lengths greater than the length at occlusion. The passive stiffness of jaw muscles was estimated using a linear approximation to the passive force-length relation given in Feldman and Orlovsky (1972). It was also assumed that passive stiffness scales linearly with physiological cross-sectional area. Using a physiological cross-sectional area of 5 cm² for cat gastrocnemius (Spector et al. 1980), estimates of passive stiffness were obtained for each modeled muscle (Table 3). The total force that a muscle can exert is thus:

$$F = M[f_1 + f_2 \text{atan}(f_3 + f_4 \dot{l}/r)] + [k(l - r)]^+ \quad (6)$$

where k is passive muscle stiffness, r is muscle length at occlusion and the four parameter arctangent function shown in square brackets represents the dependence of force on velocity. Coefficients f_1 through f_4 have values 0.82, 0.50, 0.43, 58.09, respectively.

1.1.2 Equations of motion. Sagittal plane jaw movements are described in a coordinate system that is fixed in respect to the upper skull. The origin of the coordinate system is the center of the condyle when the mandible is at occlusion. The x or "horizontal" axis is parallel to the occlusal plane and lies in the sagittal plane. The angle between the true horizontal axis and the x axis is approximately 8° (McDevitt, 1989) and is included as a constant in the simulations. In practical terms, this means that we assume that the orientation of the upper skull is fixed relative to gravity. The orientation of the jaw, α , is specified relative to the occlusal plane. Thus, the position and orientation of the jaw are given in generalized coordinates x and α .

As a simplification, we assume that the movement of the anatomical center of rotation of the condyle follows a curved path corresponding to the concave shape of the glenoid fossa and the convex shape of the articular eminence. This is described by a third-order polynomial of the variable x :

$$y = x^2(a_1x + a_2) \quad (7)$$

where a_1 and a_2 are constants characterizing the shape of the articular eminence and y is the vertical position of the center of rotation of the condyle (Fig. 3). A consequence of this simplification is that in this version of the model the vertical position of the anatomical center of rotation of the jaw is wholly dependent on its horizontal position (Baragar and Osborn 1984; Ostry and Munhall 1994).

When the condyle is at a given position along the articular eminence, the total force exerted by the muscles and by gravity on the jaw can be decomposed at the level of the joint into two components (Fig. 3), one collinear with the tangent line to the articular path at the contact point and the

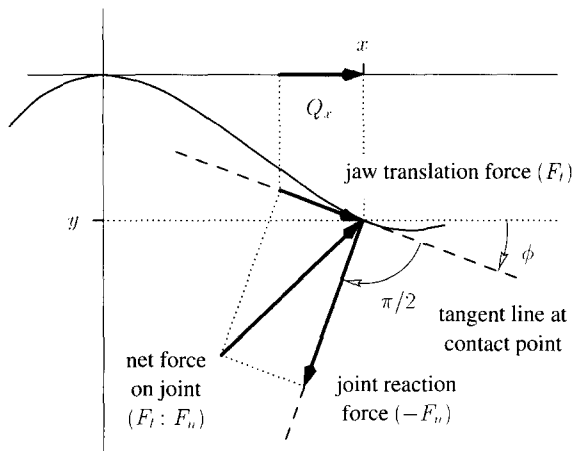


Fig. 3. Decomposition of joint forces. The polynomial approximation to the glenoid fossa and articular eminence is shown. The total force exerted by the muscles and by gravity is decomposed into a translation force which is collinear with the tangent to the articular eminence at the contact point and a joint reaction force. The translation component is projected onto the horizontal axis (Q_x)

other perpendicular to that line. The latter component will be counteracted by the joint reaction force while the former one will be responsible for the forward or backward translation of the jaw. The tangent component can be projected onto the horizontal axis (Q_x). The variable x represents the position of the jaw and Q_x is the generalized force for this variable. A generalized torque on the jaw about the center of rotation of the condyle, Q_α , may also be computed where α is the orientation angle of the jaw. The generalized force and the generalized torque take into account the contribution of all muscles attached to the mandible and the gravitational force. Similarly, Q_{xh} and Q_{yh} , the generalized forces acting on the hyoid bone, reflect both muscular and gravitational forces. (See Fig. 4 for a schematic representation of the generalized forces and generalized torque, and the jaw and hyoid coordinates.)

We use the Lagrangian approach to obtain the equations of motion (see Appendix).

1.1.3 Command vectors. We have previously introduced a vector representation of central commands for the control of jaw and multi-joint arm movements (Feldman et al. 1990; Flanagan et al. 1990). In the case of the jaw model, the essence of the vector representation is the idea that invariant commands may be defined in each of the kinematic degrees of freedom of the jaw and hyoid system. Each invariant command corresponds to a vector in λ space which will produce motion in only one degree of freedom regardless of the starting configuration of the jaw and hyoid bone. Changes in vector commands have the following general form, shown here in the context of the central command for jaw rotation:

$$A_\alpha = E_\alpha (p_{p\alpha} \hat{\lambda}_p + p_{c\alpha} \hat{\lambda}_c + p_{a\alpha} \hat{\lambda}_a + p_{t\alpha} \hat{\lambda}_t + p_{o\alpha} \hat{\lambda}_o + p_{r\alpha} \hat{\lambda}_r + p_{d\alpha} \hat{\lambda}_d) \quad (8)$$

where the $\hat{\lambda}_s$ are unit vectors associated with the direction of commands for protruder (p), closer (c) and other muscles

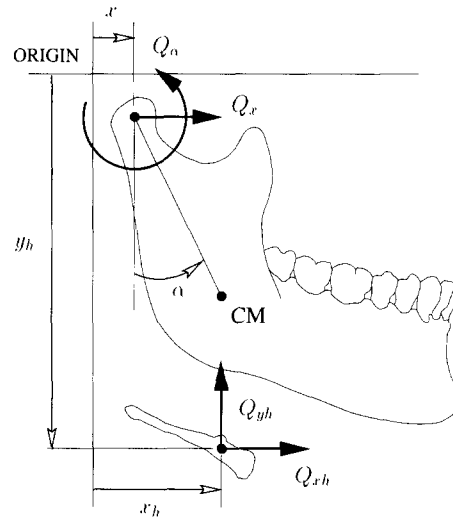


Fig. 4. Coordinates and generalized forces for the jaw and the hyoid bone. Q_x and Q_α are the generalized force and torque for the jaw; Q_{xh} and Q_{yh} are the generalized horizontal and vertical force for the hyoid bone. The origin of the coordinate system is the position of the condyle center at occlusion. The jaw position and orientation are given by x and α , where α is the angle between the vertical axis and the line connecting the condyle center to the center of mass of the jaw (CM). x_h and y_h are the horizontal and vertical position of the hyoid

in λ space. $p_{p\alpha}$, $p_{c\alpha}$, and so forth, are constant coefficients for each muscle associated with motion in a specific degree of freedom (in this example, jaw rotation, α) and E_α corresponds to the magnitude of the command (see Table 1 for definition of symbols). Vector commands are thus constant in terms of direction in λ space. Movements of different amplitude are produced by changing the magnitude of the scaling factor E_α . An overall schematic of the model showing how the amplitudes of the invariant commands are transformed into muscle λ s is provided in Fig. 5.

A fundamental problem in defining vector commands is that direction of muscle forces and muscle moment arm lengths change with jaw and hyoid position. Thus, when the same command is used in different parts of the jaw/hyoid workspace, the resulting magnitude of the movement may vary. In addition, unintended movements may arise in other degrees of freedom. Nevertheless, a fundamental question addressed by the model is whether vector commands can be defined which produce essentially independent control of each degree of freedom and which are the same regardless of changes in musculo-skeletal geometry. This would, in effect, eliminate the need for the nervous system to maintain an explicit model of musculo-skeletal geometry in planning movements.

Consider this issue in more detail. Since there are seven muscles with which to define a position in the four degree of freedom jaw and hyoid space, each static configuration in the workspace can be obtained with an infinity of combinations of λ s (the redundancy problem). This set of points in the λ space, associated with a specific configuration of the jaw and hyoid bone, will be called the *no-motion manifold*. A pure command, for example, for jaw rotation alone or jaw translation alone, may thus be defined in terms of λ shifts between no-motion manifolds whose associated mechanical

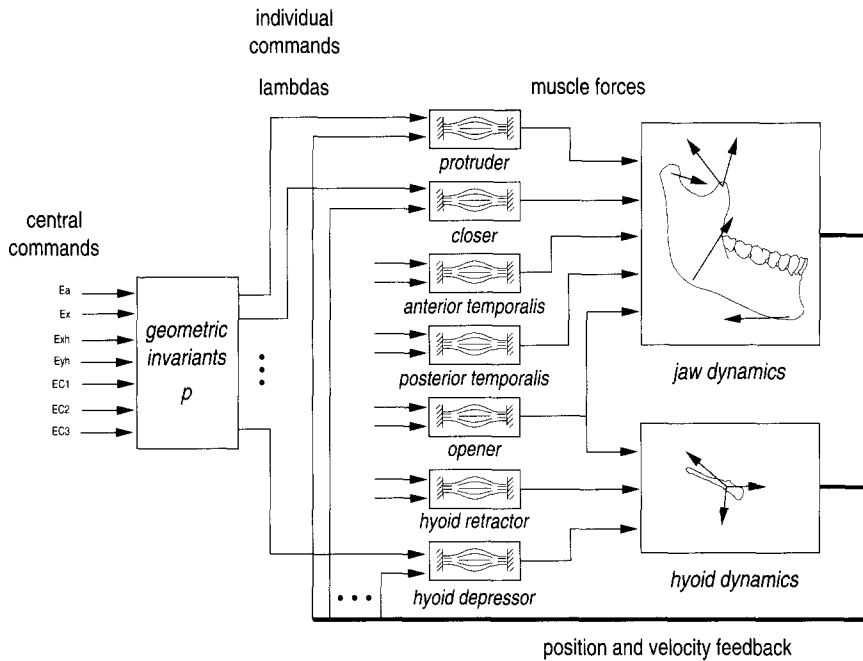


Fig. 5. Schematic representation of the model implementation. The jaw and hyoid dynamics blocks have muscle force as input and muscle length and rate of change of muscle length as output. Muscle blocks provide force output as determined by muscle length, rate of change of muscle length, and MN recruitment threshold (λ). The λ for each muscle is a linear combination of the invariant command amplitudes plus the λ values at occlusion. This applies both to commands specified in the system’s mechanical degrees of freedom (E_α , E_x , E_{xh} , and E_{yh}), and to co-contraction commands (EC_1 , EC_2 and EC_3). The coefficients of these linear combinations form a 7×7 matrix of geometric invariants [see (8)]

configurations differ only with respect to that degree of freedom for which the pure command is defined.

A graphical example of the procedure used to obtain pure commands for a given configuration in the workspace is shown in Fig. 6. An initial set of λ combinations associated with a specific jaw/hyoid configuration is referred to as the initial manifold. To obtain this manifold, we start by defining a set of four equations of generalized forces including gravity and torques which give neither rotation nor translation of the jaw/hyoid system at a specified point in the workspace. That is:

$$\begin{aligned} Q_x &= 0 \\ Q_\alpha &= 0 \\ Q_{xh} &= 0 \\ Q_{yh} &= 0 \end{aligned} \tag{9}$$

The solution of this under-determined system of four equations in the seven-dimensional space of muscle forces provides us with the no-motion manifold. It also gives us all possible combinations of muscle forces associated with a specific static configuration of the jaw and hyoid bone. This no-motion subspace is linear and has dimension 3.

To determine the direction of vectors from one manifold to the next which produce motion in an individual degree of freedom, we sample points along the no-motion manifold in force space about the point on this manifold that corresponds to the minimum sum of forces in all muscles. This starting point is used simply to obtain forces in the physiological range.

The muscle λ s associated with each of the sampled force combinations are computed easily from muscle lengths and forces using the inverse of (4). The set of λ s defines a manifold of dimension 3 in λ space although not necessarily a

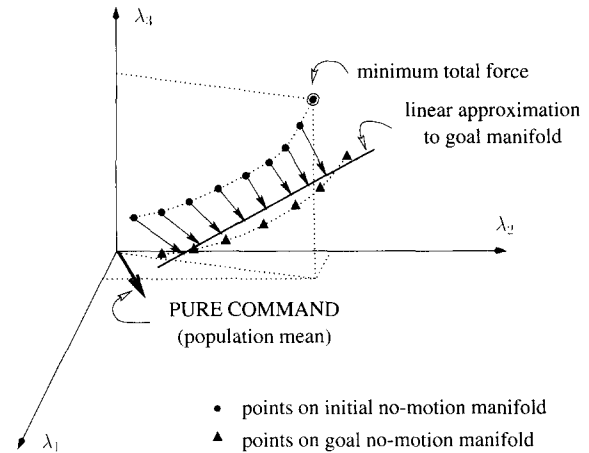


Fig. 6. Graphical example of the procedure used to define pure commands. This hypothetical example has three muscles and one mechanical degree of freedom. The circles are points on the initial manifold and the triangles represent points on the goal manifold. After finding a linear approximation to the goal manifold, the shortest vector connecting each point on the initial manifold to the linear approximation to the goal manifold is obtained. The pure command is the population mean of all of these shortest vectors

linear one (see Fig. 6 for a schematic). From each point on the initial manifold, the shortest vector to a linear approximation of the goal manifold is obtained. (The reason we need a linear approximation is that the discrete set of points which define the goal manifold must be approximated by an analytical function in order to calculate the distances.) Commands in λ space are then derived as the population mean of all these shortest vectors.

For each pure command, such as jaw rotation alone, or jaw translation alone, this procedure is repeated for configurations throughout the jaw/hyoid workspace. The population mean of the command vectors from each point in the workspace defines a single pure command which is used in the simulations presented in this paper.

2 Results

In this section, we show that invariant command vectors for jaw and hyoid motion defined above are such that (1) movements may be specified independently in each of the system's kinematic degrees of freedom, (2) the same control signals produce essentially the same result for motions in any part of the jaw/hyoid workspace, (3) control signals may be superimposed to produce combined motion in all the degrees of freedom of the jaw/hyoid system, and (4) specific command vectors may produce co-contraction of muscles without the system's motion. We also present a comparison of empirical and model data for both jaw and hyoid movements.

2.1 Effects of pure commands

Modeled central commands for the four degrees of freedom of the jaw/hyoid system were obtained using the procedure described in the preceding section. Commands for jaw rotation, jaw translation, hyoid vertical translation and hyoid horizontal translation were each expressed in terms of constant changes in the λ s of each of the modeled muscles.

Figures 7 and 8 show the effects of the pure jaw motion commands throughout the jaw/hyoid workspace. In each figure, pure commands of equal magnitude are used. Each individual point represents the jaw position and orientation achieved as a result of one of the pure command vectors. At each jaw orientation and position, the same pure command is used for nine different hyoid positions and ten different points on the no-motion manifold (90 points in total in each cluster). This enables us to examine the effect of the command over the full jaw/hyoid workspace. Each starting configuration of the jaw is shown with a small circle and a vector average of the resulting configurations with a continuous line.

Examination of the figures shows that each of the jaw commands provides a reasonable approximation to one degree of freedom motion. Typically, the pure commands result in the least departure from motion in a single degree of freedom for positions near the center of the workspace. The variability is small but systematic; the cluster orientations change with position in the workspace. The commands for hyoid motion yield results comparable to those for the jaw (see below).

We assessed in a number of ways the adequacy with which pure commands produce independent motion in the system's degrees of freedom. The pure command vectors were obtained by averaging over individual vector directions. Figure 9 shows for each command separately the distribution of individual vector directions about the vector population mean. It can be seen that in each case the range of

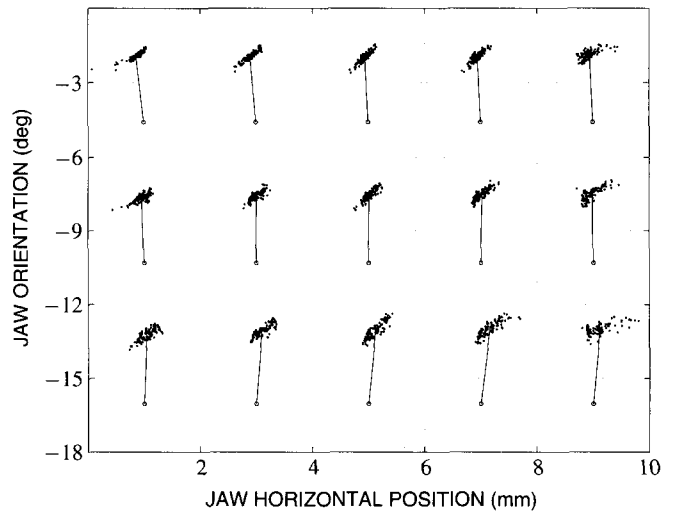


Fig. 7. Pure jaw rotation command. The individual points show the jaw orientation and position resulting from a 0.05 rad pure rotation command. For each initial jaw orientation and position shown in the figure, the command is tested for different combinations of hyoid position and total force level (different points on the no-motion manifold). The points on the no-motion manifold are obtained using a gaussian sampling procedure with a standard deviation of 10 N about the point of minimum total muscle force. The sampling is carried out in force space and the results are converted to positions in λ space

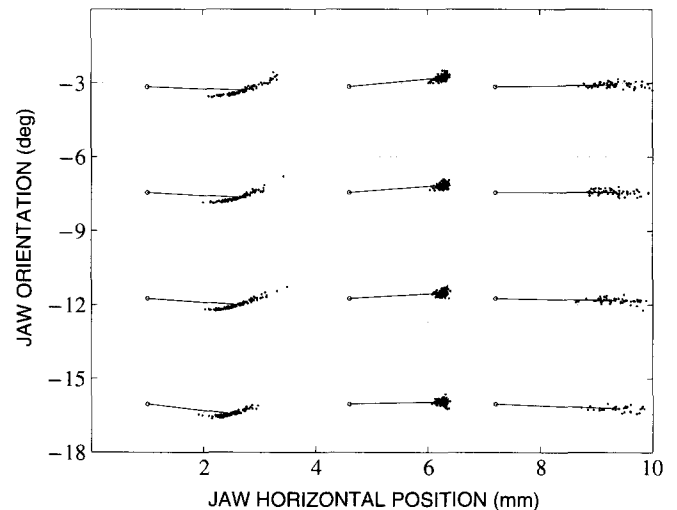


Fig. 8. Pure jaw translation command. The figure shows a 1.8 mm pure translation command

angles between individual vectors and the population mean is small. Most individual vectors fall within 10 degrees of the population mean. This suggests that for each degree of freedom represented in the model, a single pure command vector is sufficient to characterize the modeled motions.

We assessed the orthogonality of the pure command vectors directly by computing the angle between these vectors taken two by two. The resulting angles are given in Table 4. The table shows that the commands for jaw motion and for hyoid vertical translation are essentially orthogonal. The command for horizontal hyoid translation is not strictly orthogonal to the jaw commands.

The four pure command vectors define a subspace of dimension 4 in the seven-dimensional λ space. Three addi-

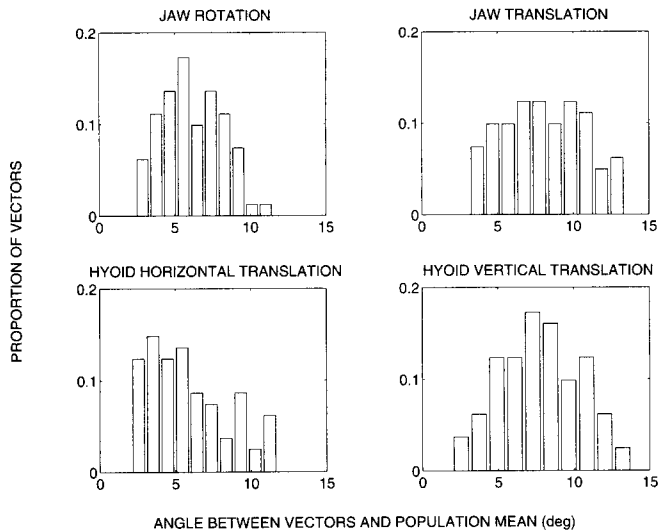


Fig. 9. The distribution of angles between individual vectors and the vector population mean for each command separately. The small range observed in each case suggests that each of the pure commands effectively accounts for all of the variance in vector directions associated with motion in that degree of freedom

Table 4. Angles between pure command vectors (A) in degrees

	A_x	A_α	A_{xh}	A_{yh}
A_x	0°	88.3°	111.9°	90.3°
A_α		0°	122.3°	102.7°
A_{xh}			0°	96.3°
A_{yh}				0°

Subscripts: x , horizontal jaw position; α , jaw orientation; xh , hyoid horizontal position; yh , hyoid vertical position

tional vectors which are orthogonal to the four pure command vectors can also be defined and these form a three-dimensional *co-contraction subspace* (Fig. 5). Different linear combinations of the co-contraction vectors correspond to different levels of total muscle force. The application of any combination of these co-contraction vectors to any equilibrium configuration of the system is expected to produce minimal motion, but will result in a change to the level of *coactivation*, that is, to the level of total muscle force. Figure 10 shows the effect of one of these three commands. The other two yield comparable results. Each cluster corresponds to jaw positions and orientations which result from the application of the command at different hyoid positions and points on the no-motion manifold.

2.2 Comparison with empirical jaw movements

In this section, we present a comparison of jaw motion paths and trajectories recorded empirically (Bateson and Ostry, 1995) and simulated paths and trajectories obtained using constant rate shifts in the equilibrium jaw orientation and equilibrium jaw position.

Figure 11 provides empirical patterns of jaw rotation and translation during repetitions of the utterance *isisa*. The modeled equilibrium shifts and predicted kinematics are also shown. Jaw motion paths from the same data set are shown in Fig. 13. Jaw orientation in the sagittal plane is plotted as

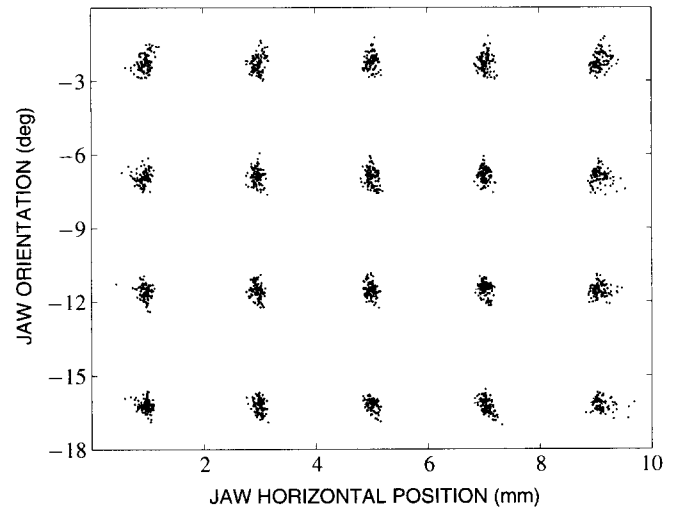


Fig. 10. The effects of one of three co-contraction vectors. The figure shows variation in jaw position and orientation resulting from the use of the co-contraction command. Individual points are obtained for different hyoid positions and different points on the no-motion manifold

a function of horizontal jaw translation. The paths presented here are for the syllables *si*, *shi*, *ri*, *li*, *ti*, *ki*, *pi* and *fi* produced at a normal speech rate. For each of the paths shown in the figure, the movement starts at the top left with the production of the consonant and ends at the bottom right at maximum jaw aperture during vowel production. The figure shows that empirically measured jaw paths in joint coordinates form straight lines (lower panel). The paths for different speech sounds may be translated forward independent of the slope relating rotation and translation and may likewise be rotated downward, again independent of the rotation-translation slope. An instance of pure jaw translation is also observed. Note that final jaw positions and orientations differ for different syllables even though the associated vowel is unchanged. This is because the production of the vowel *i* involves a coordination of jaw and tongue motion. The location and magnitude of the palatal constriction achieved by the tongue is relatively constant for the vowel *i*, although jaw position and orientation may vary depending on the consonantal context.

The simulations presented in Figs. 11 and 13 test the idea that the empirically observed straight line paths obtained when jaw rotation is plotted against horizontal jaw translation arise when joint equilibrium orientations and positions start to shift simultaneously and each shifts at the same relative velocity (Ostry and Munhall 1994). It is seen that the time-varying kinematics and the jaw motion paths are satisfactorily approximated by this assumption. Note as well that the smooth changes in jaw position and orientation may be simulated using constant rate changes in the jaw equilibrium angle and jaw equilibrium position.

2.3 Empirical and modeled jaw and hyoid motion

Empirical and modeled patterns of jaw and hyoid motion are shown in Fig. 12. The data, reported in Westbury (1988), were obtained from cineradiographic recordings. We show

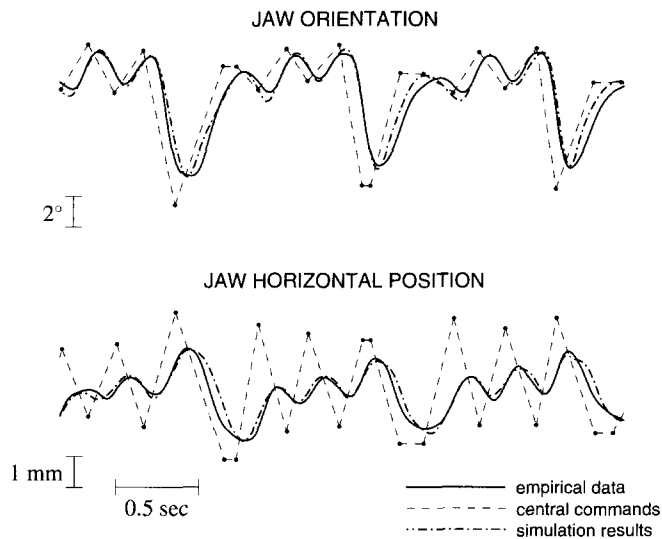


Fig. 11. Empirical and model data during repetitions of *isisa*. The hyoid bone is at the assumed rest position for occlusion throughout the simulated movement

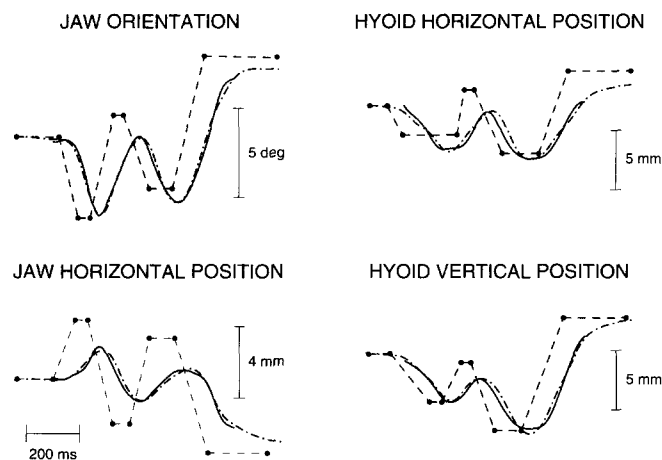


Fig. 12. Motion of the jaw and hyoid bone in speech. Empirical and model data are shown. The labeling conventions are the same as in Fig. 11. *Continuous lines* are empirical data; *dashed lines* are central commands. Simulated results are shown with *alternating dots and dashes*

the jaw orientation and position and the vertical and horizontal position of the mid-point of the hyoid bone. (Note that jaw position and orientation were not reported directly but could be derived from data presented in the paper.) The sequence shown here is for the utterance *padap*. As the jaw rotates downward, the hyoid is lowered and retracted. The jaw opener muscles thus lengthen as they contract to lower the jaw. Constant rate equilibrium shifts are tested for each command. Smooth and gradual shifts similar to those obtained empirically are observed in the predicted kinematics.

3 Discussion

We have presented a model of human sagittal plane jaw and hyoid motion. The aim was to assess the form of central control signals to the jaw/hyoid system and how they are coordinated in the context of the redundancy in the number

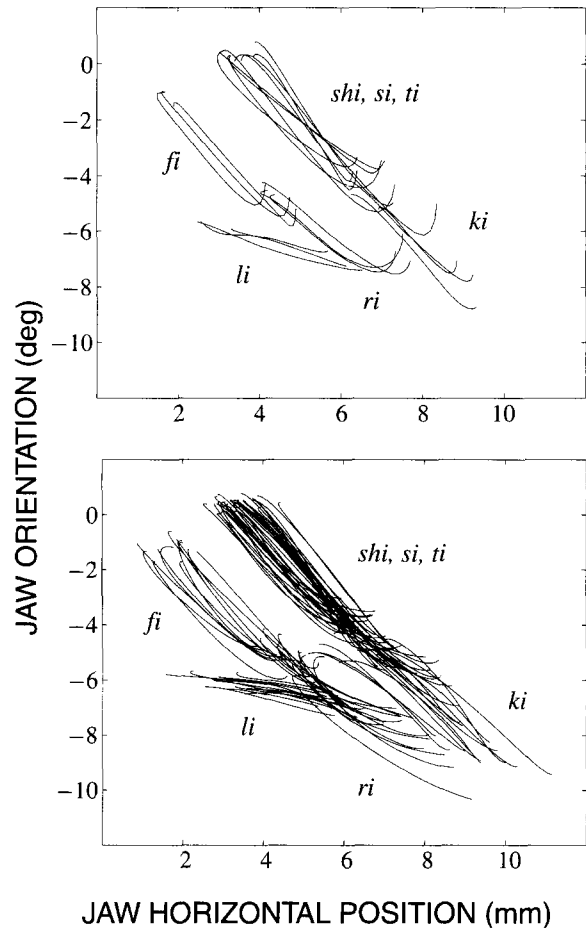


Fig. 13. Jaw motion paths in speech. Jaw rotation is plotted as a function of horizontal jaw translation. Both empirical (*below*) and model data (*above*) are shown. Note that jaw motion paths form straight lines in joint coordinates

of muscles and the essential non-linearity in the system's musculo-skeletal geometry.

Consistent with empirical findings (Ostry and Munhall, 1994), we show that command vectors can be defined to produce essentially independent motions in individual degrees of freedom. The small but systematic errors in jaw and hyoid position and orientation are the consequence of using a linear relationship between the commands and the muscle λ s to control a system with non-linear geometry. However, our simulations demonstrate the plausibility of the idea that the nervous system need not recompute control signals to produce the same movements in different parts of the workspace. This suggests that the nervous system may not take explicit account of muscle and skeletal geometry, that is, of position-dependent changes in muscle force direction and muscle moment arm lengths, in planning movements. We do not want, however, to say that the geometry is entirely ignored in the control of the jaw and hyoid. Obviously, the coefficients in the linear decomposition of command vectors, although invariant, are defined by the jaw/hyoid geometry. Different geometries, for example those of the arm or the hindlimb, may be associated with different control invariants.

The properties of commands were evaluated in a number of ways. Figures 7 through 10 show that the pure command vectors account well for motions throughout the jaw/hyoid workspace. The angles between these pure command vectors indicate that the commands are essentially mutually orthogonal. An examination of the predicted time-varying kinematics of jaw motion resulting from pure commands shows that the commands are largely orthogonal during the course of the movement as well. Variability in the positions and orientations of the jaw and hyoid bone resulting from pure commands was in all cases small in comparison with the magnitude of equilibrium shift resulting from the pure commands.

The ability to define invariant command vectors appears to arise from the *approximate* linearity of the no-motion manifold in λ space. We have completed a preliminary assessment of the linearity of this manifold using principal components analysis, a linear decomposition technique. Principal components analyses were carried out for 100 points on the λ space no-motion manifold at a position in the middle of the workspace. The analysis revealed that three factors accounted for essentially all the variance associated with the actual three-dimensional no-motion manifold. This suggests that the no-motion manifold is itself close to linear in λ space. The reason that vector commands defined on the basis of shifts between no-motion manifolds give non-constant results is because the no-motion manifolds, although almost linear, are not parallel. This is primarily because of the non-constant muscle moment arms and non-constant lines of muscle action throughout the workspace.

In order to define pure commands we sampled combinations of jaw and hyoid position and orientation. Some of these combinations may never actually occur but were examined anyway to test whether commands could be defined which are essentially orthogonal throughout the workspace. In effect, this procedure sets an upper limit to errors associated with the use of pure commands. Any procedure which further restricts the set of jaw and hyoid combinations used to define the pure commands will of necessity obtain results whose variability is less than reported here. The actual boundaries of the real workspace are probably smaller than those tested in this paper. Figure 13, which shows movements recorded over a wide range of speech movements and a loud speech volume, probably provides a good first approximation.

Comparisons of empirical data and model simulation results were provided for both jaw motion alone and for combined jaw and hyoid motion in speech. Our present results are consistent with the idea that in the case of jaw movements, straight line paths in joint coordinates arise because changes to jaw equilibrium orientations and positions both start and end at the same time and maintain the same relative velocity. The results also demonstrate that constant rate control signals can account for the smooth gradual motions which are actually observed. Smoothness of movement may thus arise from motion dynamics and need not be planned directly as part of the movement.

Although the jaw and limb control systems are different in many aspects, the principles of sensorimotor integration underlying the λ model may be equally applicable to both. To clarify this, several points should be emphasized. First,

the existence of positional feedback to MNs is critical to the model. On the other hand, whether this feedback is mono- or polysynaptic, or whether this feedback is provided by muscle spindles or other proprioceptors is not. Thus, although jaw opener muscles contain few muscle spindles, reflex facilitation of jaw opener MNs has been demonstrated in a number of ways (Lamarre and Lund 1975; Hellsing 1977; Neilson et al. 1979; van Willigen 1986).

According to the model, motor control is associated with the regulation of the MN recruitment threshold, λ . This regulation may be produced by pre- or postsynaptic inputs to α -MNs or, indirectly, by changing the activity of γ -MNs. Changes in λ define a total measure of these influences on MNs. In different motor systems, the same changes in λ s may be achieved by different combinations of inputs. For example, muscle spindle afferents of closer muscles are mostly active during the opening phase of mastication (Goodwin and Luschei 1975). The facilitation of closer muscle MNs from these afferents is counteracted by large hyperpolarizing potentials during the opening phase (Goldberg and Tal 1978). In the model, this hyperpolarizing potential may be associated with an increase in the threshold of the stretch reflex. However, the model suggests that this reflex may still be functional if jaw opening exceeds a specific limit.

The model suggests that invariant vector commands (the co-activation command and four types of commands associated with motion in different degrees of freedom) may be produced in different combinations depending on motor tasks. This assumption is consistent with the finding that muscle activation patterns in speech involve co-activation of closers and openers, in contrast to the highly reciprocal pattern observed during mastication (Moore et al. 1988). Vector commands in the model imply the existence of neurons with mono- or polysynaptic projections to MNs of practically all jaw muscles. In limb motor systems, influences of descending commands are usually mediated by interneurons of reflex loops. Whether control inputs to the jaw motor system are organized in a similar manner remains unknown. For example, the Ia interneuronal system of reciprocal inhibition from antagonist muscles established in limb muscles has not been found in the jaw motor system. Nevertheless, central commands may still be mediated by other interneurons of jaw reflex loops.

A number of simplifying assumptions in the present work should be noted. Constraints on motion due to TMJ ligaments were not modeled. These ligaments act to define the workspace boundaries. We have also treated sagittal plane motion independent of lateral jaw motions. This is consistent with the view that control signals are organized to produce independent motions in different degrees of freedom. We have assumed that the vertical position of the jaw's rotational axis is dependent on its horizontal position. We have also neglected the actions of tongue muscles on hyoid bone and jaw motions. In addition, hyoid bone rotations have not been modeled.

Although the model generally performed well, some aspects of its performance will need attention in future work. One problem was that jaw translation was typically more damped than jaw rotation. We made several attempts to correct this problem by balancing the dynamic response in these degrees of freedom better. We suspected that the source of

the problem was a mismatch in the estimates of the relative force-generating capabilities of muscles. Thus, we derived values for the magnitude scaling factor, ρ , such that, in a linear approximation to the jaw model, the natural frequencies of the jaw in rotation and translation were as close as possible. The determination of ρ s in this fashion produced no noticeable improvement. Nor did a parametric variation in the values of muscle ρ s over an order of magnitude range. Indeed we found that the system's dynamic response was probably more affected by the position on the no-motion manifold.

In the present study, we offer a solution to the problems of coordination and control in multi-muscle and multi-degree-of-freedom systems. In addition, we analyze the role of the system's geometry in these control problems. In the present paper we have focused on the jaw/hyoid system. However these solutions may equally be applied to limb movements or even movements of the entire body. They may also be relevant to robotics, which faces similar problems.

There are direct applications of the model to a number of problems in speech research. Explicit models of speech articulators are essential to the interpretation of kinematics. Without these models, kinematic patterns which are attributable to central control cannot be distinguished from those which arise due to dynamics. For example, we have used the jaw model in conjunction with empirical studies to examine the origins of observed patterns of context-sensitivity in speech kinematics (Ostry et al. 1996). We have observed that even when no account is taken of context at the level of central control, kinematic patterns vary in amplitude and duration as a function of the magnitude of the preceding or following movement in exactly the same manner as one observes empirically. Apparent sensitivity to context may thus arise from muscle mechanics and dynamics, and accordingly, these factors must be considered before drawing inferences about control or inferring planning mechanisms.

The model also provides a means of exploring the sources of variation in speech movements (Perrier et al., 1996). In simulation studies we have shown in different ways how variability in measured kinematics can arise in spite of constant-magnitude speech control signals. For example, kinematic variability may arise from a combination of the co-contraction level and dynamics, even when the equilibrium shift which underlies the movement remains constant. Variation in endpoint position may also occur when invariant commands are used. Once again, the model provides a way to separate the biomechanical sources of variability from those which are centrally controlled.

Appendix

The jaw was treated as a rigid body with distributed mass. Calling the mass of the jaw m_j , the moment of inertia of the jaw about the center of mass I , and the mass of the hyoid m_h , the total kinetic energy of the system is given by:

$$T = \frac{1}{2}m_j v_j^2 + \frac{1}{2}I\dot{\alpha}^2 + \frac{1}{2}m_h v_h^2$$

where v_j and v_h are the linear velocities of the jaw and the hyoid bone and $\dot{\alpha}$ is the angular velocity of the jaw.

The Lagrangian equations of motion for the jaw are:

$$Q_x = \frac{d}{dt} \left(\frac{\partial T}{\partial \dot{x}} \right) - \frac{\partial T}{\partial x}$$

$$Q_\alpha = \frac{d}{dt} \left(\frac{\partial T}{\partial \dot{\alpha}} \right) - \frac{\partial T}{\partial \alpha}$$

where Q_x and Q_α are the generalized forces acting on the jaw due to muscles and gravitational forces.

The accelerations for rotation and horizontal translation of the free-moving jaw are given by the following expressions, where l_j is the distance from the condyle center to the center of mass, α is the angle between the vertical axis and a line segment between the condyle center and the center of mass of the jaw, and (x_j, y_j) is the position of the center of mass of the jaw:

$$\begin{bmatrix} \ddot{x} \\ \ddot{\alpha} \end{bmatrix} = (\mathbf{DB})^{-1}(\mathbf{A} - \mathbf{E} - \mathbf{DC})$$

where

$$\mathbf{A} = \begin{bmatrix} Q_x + \partial T / \partial x \\ Q_\alpha + \partial T / \partial \alpha \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} 1 & l_j \cos \alpha \\ \partial y / \partial x & l_j \sin \alpha \\ 0 & 1 \end{bmatrix}$$

$$\mathbf{C} = \begin{bmatrix} -l_j \dot{\alpha}^2 \sin \alpha \\ (\partial^2 y / \partial x^2) \dot{x}^2 + l_j \dot{\alpha}^2 \cos \alpha \\ 0 \end{bmatrix}$$

$$\mathbf{D} = \begin{bmatrix} m_j & m_j (\partial y / \partial x) & 0 \\ m_j l_j \cos \alpha & m_j l_j \sin \alpha & I \end{bmatrix}$$

$$\mathbf{E} = \begin{bmatrix} m_j (\partial^2 y / \partial x^2) \dot{x} \dot{y}_j \\ m_j l_j \dot{\alpha} (\dot{y}_j \cos \alpha - \dot{x}_j \sin \alpha) \end{bmatrix}$$

The equations of motion for the hyoid, h , are much simpler:

$$\ddot{x}_h = Q_{xh} / m_h$$

$$\ddot{y}_h = Q_{yh} / m_h$$

where Q_{xh} and Q_{yh} are the generalized forces acting on the hyoid bone due to muscle and gravitational forces, m_h is the hyoid mass, and \ddot{x}_h and \ddot{y}_h are its horizontal and vertical accelerations.

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