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The Equilibrium Point Hypothesis and its Application to Speech Motor Control

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November 24, 1995

Accepted for publication in the Journal of Speech and Hearing Research

ABSTRACT

In this paper, we address a number of issues in speech research in the context of the equilibrium point hypothesis of motor control. The hypothesis suggests that movements arise from shifts in the equilibrium position of the limb or the speech articulator. The equilibrium is a consequence of the interaction of central neural commands, reflex mechanisms, muscle properties and external loads, but it is under the control of central neural commands. These commands act to shift the equilibrium via centrally specified signals acting at the level of the motoneurone (MN) pool. In the context of a model of sagittal plane jaw and hyoid motion based on the λ version of the equilibrium point hypothesis, we consider the implications of this hypothesis for the notion of articulatory targets. We suggest that simple linear control signals may underlie smooth articulatory trajectories. We explore as well the phenomenon of intra-articulator coarticulation in jaw movement. We suggest that even when no account is taken of upcoming context, that apparent anticipatory changes in movement amplitude and duration may arise due to dynamics. We also present a number of simulations that show in different ways how variability in measured kinematics can arise in spite of constant magnitude speech control signals.

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INTRODUCTION

A major difficulty in inferring control strategies in speech from the kinematic data characterizing human orofacial motion is the lack of physiologically based models of the underlying control. Such models can help in the interpretation of data in which the underlying control is hidden by factors such as dynamics and muscle mechanical properties. Physiological models may permit the separation of aspects of the kinematics due to neural control from those due to the biomechanical properties of the system. In this paper, we present one such physiological model, the equilibrium point hypothesis of motor control, and consider its specific application to issues in speech control.

The model is introduced in detail below. However, very briefly, the hypothesis suggests that movements arise from shifts in the equilibrium position of the limb or the speech articulator. The equilibrium is a consequence of the interaction of central neural commands, reflex mechanisms, muscle properties and external loads, but it is under the control of central neural commands. These commands act to shift the equilibrium via centrally specified signals acting at the level of the motoneurone (MN) pool.

The idea that the nervous system regulates the equilibrium of the muscle-load system has been proposed previously in speech research (Fowler, 1977; Kelso, Saltzman, & Tuller, 1986; Ostry, Keller, & Parush, 1983; Ostry & Munhall, 1994). One specific appeal of the EP hypothesis as a model of the control underlying speech motions is that the model is

grounded in basic physiological mechanisms. The model is derived from principles such as the dependence of force on muscle length and velocity. The explicit formulation of each of these principles helps to constrain the model.

In the sections which follow, we first introduce the central concepts of the EP hypothesis. We describe its application to the development of a seven muscle model of jaw and hyoid motion (Laboissière et al., in press). We explain why the model is particularly suited for the characterization of speech motor phenomena. With the aid of simulations we show (a) how the concept of equilibrium position provides insights into the concept of articulatory targets, (b) how articulatory variability can arise with the use of invariant motor commands, and (c) how some of the observed variability associated with intra-articulator coarticulation may be attributed to dynamics without the need for specific central control. (Note that “dynamics” refers to the dependence of articulator motion on muscular, visco-elastic, and inertial properties of the system. Dynamics is what arises from solving the equations of motion.)

THE EQUILIBRIUM POINT HYPOTHESIS (λ MODEL)

Since its introduction almost 30 years ago, the equilibrium point (EP) hypothesis (λ model) has been a central theory in motor control. Originally developed in the context of one joint arm movements (Feldman, 1966; Feldman, 1986), the model has now been adapted to multi-joint arm movement (Feldman, Adamovich, Ostry, & Flanagan, 1990; Flanagan, Ostry, & Feldman, 1993), eye movement (Feldman, 1981) and to human jaw movement in speech and mastication (Flanagan et al., 1990; Laboissière et al., in press). Recent work has focused on the neural substrate of the equilibrium position (Giszter,

Mussa-Ivaldi, & Bizzi, 1992), on the estimation of equilibrium trajectories (Flanagan, Ostry, & Feldman, 1993; Latash & Gottlieb, 1991), the measurement of limb impedance (Bennett, Hollerbach, Xu, & Hunter, 1992; Bennett, 1993; Gomi, Koike, & Kawato, 1992; Shadmehr, 1993), and the determinants of reflex threshold (Levin & Feldman, 1994). The model has been shown to account for a range of physiological data. This includes electromyographic patterns in one and two joint arm movements, phasic and tonic reflexes and patterns of muscle co-contraction (Feldman, Adamovich, Ostry, & Flanagan, 1990). The extension of the model to different motor systems and the effort to understand various impairments within its framework (Levin & Feldman, 1994) represents an attempt to develop a general theory of motor control (see Berkinblit, Feldman, & Fukson, 1986; Bizzi, Hogan, Mussa-Ivaldi, & Giszter, 1992; Feldman, Adamovich, Ostry, & Flanagan, 1990; Feldman & Levin, in press; Latash, 1993 for recent summaries).

Basic Control Mechanisms

Motor innervation to muscles arises from α MNs which innervate the main body of the muscle and from γ MNs which contribute to α MN excitation through reflexes (see Rothwell, 1993 for an introduction). The basis of the model is the suggestion that movement arises from changes to neural control signals which shift the equilibrium state of the motor system. The essential control variables are independent changes in the membrane potentials of α and γ motoneurons (MNs) which establish a threshold muscle length (λ) at which the recruitment of MNs begins. Muscle activation and hence force vary in relation to the difference between the actual and the threshold muscle lengths and the rate of muscle length change. Thus, by shifting λ through changes to the central

facilitation of MNs, the system can produce movement to a new equilibrium position.

The central notions in the model are shown in Figure 1 in the context of a single jaw muscle and load. For simplicity, we will focus on a jaw closer muscle (depicted in black) and on the load due to the gravitational force. The panel on the left shows a number of different jaw configurations. The corresponding depolarization of α MNs is shown at the top right. The horizontal line gives the threshold for MN recruitment. The descending input to the MN provides the level of central facilitation which may be specified independent of muscle length. Afferent facilitation also contributes to the depolarization of the MN and varies directly with muscle length. Thus, while the equilibrium position is essentially under central control, the activation level of the MN reflects a net contribution which includes both the direct descending input to the MN and indirect input due to afferent pathways (see Appendix).

In (a), we see, in the left hand panel, the subject resting horizontally with the system in equilibrium at a position near to occlusion. The level of total depolarization, as seen in the top right hand panel, exceeds the threshold level and the load due to gravity is supported by an overall level of central and afferent activity. When the subject changes to a vertical position (b), the load acting to extend the jaw closer muscle increases. This increases the level of muscle-length dependent afferent facilitation of the MN pool which in turn acts to establish a new equilibrium position. Note, that the level of central facilitation is unchanged by these changes in load even though the total level of MN activation is changed.

The lower right hand panel of Figure 1 demonstrates these characteristics in terms of the muscle's force-length curve. The variable λ gives the muscle length at which motoneurone

recruitment begins. The exponential shape of the force-length relation reflects the well known size-principle for MN recruitment such that as the difference between the actual and threshold muscle length progressively increases, progressively larger motor units with larger force outputs are recruited (Henneman, Somjen, & Carpenter, 1965). At muscle length l , a force equal to F is generated which balances the load (a). A change in the position of the head relative to the gravitational force loads the jaw and stretches the muscle to length l' . The length dependent afferent facilitation results in the recruitment of new motor units which increases force to F' (b). At this point the muscle force balances the load force. To summarize, changes in load which result in muscle stretch (or unloading) lead to the recruitment (or derecruitment) of motor units as a result of changes in length dependent facilitation to the MN pool. The measure of independent central control, λ , is unaffected even though both force and muscle length are changed.

As shown by comparing (b) and (c), the model suggests that voluntary movement arises as a consequence of increases in the level of central facilitation to the MN pool. Increases in facilitation depolarize MNs and result in the recruitment of additional motor units. This increases total force and results in muscle shortening. As the muscle shortens, the facilitation to the MN pool due to length dependent afferent input decreases and a new equilibrium is established. Voluntary movements are depicted in the lower right hand panel in terms of the muscle's force-length relation. At (b), the threshold muscle length is λ , and the weight of the jaw is supported by muscle force F' at muscle length l' . By increasing central facilitation, the threshold length for MN recruitment is reduced from λ to λ' . As λ shifts, the difference between the actual and threshold muscle length increases, more MNs are recruited and the muscle begins to actively shorten. As the threshold length reaches λ' , the jaw achieves a new equilibrium state in which muscle force is F' and muscle length is l

(c). The movements which arise from changes to the independently specified parameter λ thus depend on both direct central facilitation to the MN pool and facilitation arising from afferent input to the MN.

The physiological mechanism which we have just described provides the means to produce specific movements through various combinations of λ s. Figure 2 shows a simplified demonstration of how movement may arise in a system with antagonistic muscles. This is illustrated with the jaw closer muscle, masseter, and the jaw opener muscle, anterior digastric (both depicted in black). The masseter produces jaw closing torques, T_c , and the anterior digastric produces jaw opening torques, T_o , in the opposite direction. Through the specification of λ s for jaw closer and jaw opener muscles, an equilibrium joint angle, α , is determined where the net joint torque is zero, that is, where the joint torques of the two muscles are equal in magnitude but in opposite directions (see top right panel). λ s also provide independent control of joint stiffness or muscle co-contraction, represented by the slope of the line which gives the sum of the torques, T_c and T_o (labelled total torque in the figure). If the λ s for opener and closer muscles are shifted in the same direction (middle panel), the equilibrium angle changes from α to α' without affecting joint stiffness. Alternatively, if the λ s for closers and openers are shifted by equal amounts in opposite directions (bottom panel), then joint stiffness increases while the equilibrium joint angle is unchanged. Thus, both the equilibrium angle, α , and the level of co-contraction can be specified with combinations of λ s.

A number of points about the model should be emphasized. It should be noted that there is a major difference between the λ model and Merton's (Eldred, Granit, & Merton, 1953) account in which proprioception also plays a central role. Whereas α MN activation in the λ model reflects both direct central input to α MNs and afferent facilitation due to reflexes,

in the Merton account, neural commands act upon γ MNs; α MN activation arises indirectly through reflexes. Also note, that according to the λ model afferent input to α MNs varies continuously with extrafusal muscle length. This continuity, in the case of muscle spindle afferents, is provided by coordinated central control signals to α and γ MNs. Although we do not distinguish in the version of the jaw model presented below, the central control of α and γ MNs, elsewhere we have described a formulation with separate α and γ control signals (Feldman, Adamovich, Ostry, & Flanagan, 1990). The description of the λ model presented above focuses on the contribution of spindle afferent information to α MN excitation. Non-spindle afferents may also provide this facilitation and are wholly compatible with the model (see Discussion).

The model suggests that muscle afferent input plays a role both in movement production and in posture. The demonstration by Cooker, Larson, & Luschei (1980), that the stretch reflex in jaw closer muscles contributes significantly to the postural stability of the jaw is consistent with this suggestion. However, Goodwin & Luschei (1974) have also demonstrated that few changes occur in jaw movement patterns or EMG activity during mastication in monkeys following the elimination of proprioceptive input from muscle spindle afferents (also see Dellow & Lund, 1971). Although the λ model places considerable emphasis on the role of proprioceptive inputs in motor control, it should be noted that the Goodwin & Luschei (1974) findings are not inconsistent with the λ model. The model suggests that a combination of central commands and afferent feedback determine the equilibrium state. Thus the nervous system can specify desired positions using central commands alone, without the need for afferent feedback.

The Jaw Model

While control is governed by central commands, it is desirable in models of the orofacial articulators to include a sufficient formulation of their mechanical and geometrical properties. One of the goals in modeling orofacial function is to study the form of central nervous system (CNS) commands which underlie the kinematic observables. Consequently, in order to understand control on the basis of kinematics, it is useful to be able to separate control signals from the system's biomechanics. Modeling the elaborate geometry and dynamics of the orofacial articulators is helpful, not because of a specific interest in their characteristics, but because it is otherwise difficult to relate control signals to the resulting kinematics which may be measured empirically.

With this aim, we have recently developed a model of sagittal plane jaw and hyoid motion based on the EP hypothesis (Laboissière et al., in press). The model, which is implemented as a computer simulation, has seven muscles (or muscle groups). Consistent with empirical evidence (Bothorel, 1975; Ostry & Munhall, 1994), the control signals in the model are organized into a set of commands, which control motion in four kinematic degrees of freedom (jaw rotation, horizontal jaw translation, vertical hyoid translation, horizontal hyoid translation). The application of these commands results in changes to the MN recruitment threshold of individual muscles and enables the independent production of motion in each of the four controlled degrees of freedom. The level of co-contraction is also controlled. These control signals (at the level of degrees of freedom) may act alone or in combination.

Figure 3 shows the layout of the model. Neural control signals (Λ) which are associated with changes in values of the system's four degrees of freedom are each mapped onto

control signals at the level of individual muscles (λ). This corresponds to a time varying facilitation to the MNs of each muscle. As described above, the muscle activation and force depend on the difference between the threshold muscle length and the current length as well as on the rate of muscle length change (see Appendix). Muscle length and velocity information are provided by afferent input to MNs following a reflex delay. The elements in each of the muscle blocks in the figure correspond to individually modelled muscle mechanical properties. These include muscle properties such as the dependence of force on muscle length and on passive elastic properties and the graded development of muscle force due to calcium dependent muscle kinetics. Mechanical damping is provided by velocity dependent reflex inputs and muscle intrinsic properties. The force arising in each muscle contributes to the production of jaw and hyoid forces and torques. These act through the system's equations of motion to produce changes in jaw and hyoid position and orientation. There are separate jaw and hyoid dynamics and realistic musculo-skeletal geometry.

The model thus provides a way to study human jaw motions in speech in a manner which integrates biomechanical characteristics and the underlying control. The model can also make explicit predictions concerning muscle activation patterns which may be tested (see Appendix). In the following section we will discuss the significance of a number of properties of the λ model and then, using simulations with the jaw model, show their implications for the control of speech.

SENSORIMOTOR TRANSFORMATIONS IN SPEECH

Because of the acoustical nature of the speech signal, speech researchers have been inclined to characterize speech production in terms of its acoustical and auditory correlates.

However, regularities in vocal tract shape are also observed. Thus, while it appears that speech is organized to satisfy perceptual requirements, a mapping presumably exists between sound classes defined at the auditory level and the organization of articulatory movements. One of the main challenges in speech research is to understand the relationship between speech as a perceptual phenomenon and speech organized with respect to orofacial motion.

Several researchers have presented evidence which sheds light on the nature of the relationship between auditory and articulatory levels in speech. Lindblom, Lubker, & Gay (1979) and Gay, Lindblom, & Lubker (1981) report bite-block experiments in which speakers were required to produce isolated vowels immediately after the insertion between the teeth of a block which forced the jaw to assume an unusual position. The authors report that speakers were able to produce the standard formant patterns for these vowels, by moving the tongue in such a way that the oral constriction location and area remained the same as in the unperturbed conditions. These data suggest that, in vowel production, the perceptual goal is reached via control at the articulatory level in terms of specific geometrical features of the vocal tract, namely the characteristics of the constriction.

The idea that the speech task may be specified in terms of the geometry of the vocal tract is supported by simulation studies reported by Boe, Perrier, & Bailly (1992). These authors used an anthropomorphic articulatory model of the vocal tract in order to study articulatory to acoustic relationships in vowel production. They report regularities relating acoustical patterns for French vowels to the oral constriction location and area, and the area of the lip aperture. This again suggests that vocal tract geometry and hence articulatory movement are part of the control space in speech.

Perkell et al. (1993) published articulatory data on the English vowel [u]⁹⁸ which suggested that orofacial motions in speech are not organized in terms of the separate control of individual geometrical features. These authors report variability over repetitions in lip aperture as well as in tongue position. These variations are correlated such that as lip aperture increases, more posterior tongue positions are observed. Orofacial motions thus appear to be coordinated in a manner which is oriented towards the preservation of the auditory effect. Savariaux, Perrier, & Orliaguet (in press) demonstrate that coordination of the sort reported by Perkell et al. (1993) is only possible within certain limits: large modifications to tongue shape could not be achieved, without extensive training, to adjust for the perturbation due to the insertion of a tube between the lips. This suggests that there are a limited range of articulatory patterns associated with a specific perceptual effect.

Since articulatory organization is a central aspect in the control of speech it is useful to have a formal model of this organization. The equilibrium point hypothesis provides such a model and one which is well suited to speech. The control signals in the model are organized in space and time and these are the salient variables in speech production strategies. Moreover, the model provides an account of how articulatory movement can be achieved with the accuracy required for speech. For example, the acoustic distinction between [i]⁹¹ and [e]⁹² depends upon a slight difference in tongue shapes (Majid, 1986). A one millimeter error in the distance between tongue and hard palate can be responsible for the incorrect production of an alveolar fricative (Shadle, 1985; Shadle & Scully, 1995). The model suggests that afferent facilitation to MNs due to short latency reflex input and also long latency input contributes to the achievement of final position.

Short latency somatosensory feedback could thus be valuable in a speech production

system in which auditory input may not be used in ongoing control. Since vowels have a mean duration of approximately 80 ms and consonants have mean durations around 40 ms (O'Shaughnessy, 1981), long latency auditory feedback related to the identity of the sound is likely to play a limited role at the segmental level in speech. This is supported by experimental work showing that speakers can produce intelligible speech even after hearing loss (Lane & Wozniak, 1991; Manzella et al., 1994). This is also supported by work on stutterers and normal speakers showing that delayed auditory feedback in the range of 50 ms to 200 ms effects prosodic (speaking rate, fundamental frequency, speech intensity, fluency) rather than segmental features (Hargrave, Kalinowski, Stuart, Armson, & Jones, 1994; Lechner, 1979; Siegel & Jr., 1974; Stager & Ludlow, 1993). In contrast, proprioceptive feedback from orofacial muscle spindle receptors and other somatosensory afferents, because they are far faster, may be used in segmental control. Unloading responses in human jaw opener and jaw closer muscles have latencies of 10 to 20 ms (Lamarre & Lund, 1975). Feedback signals of this latency presumably play a role in the ongoing control of speech articulator motion.

INVARIANCE AND VARIABILITY IN SPEECH

The Relationship between Central Commands and Articulator Positions

According to the model, movements are effectively changes in posture, that is, shifts in the equilibrium state of the system. We suggest that the control of speech may be related to specific postures of articulators and that posture and successive changes in posture

correspond to a representation of the articulatory task at the level of control.

We illustrate this notion by using simulations based on the jaw model. In this model, since the four degrees of freedom of the jaw and hyoid bone depend on the state of seven muscles, there is an infinity of combinations of muscle λ s associated with any static geometrical configuration. We have called the set of points in λ space that correspond to a given position of the jaw and hyoid, the no-motion manifold. Thus, each point in the jaw / hyoid workspace may be associated with a specific no-motion manifold and movements may be defined in terms of λ shifts between manifolds.

A schematic of no-motion manifolds is given in Figure 4. Although the no-motion manifolds in the jaw model are actually three dimensional in λ space, for illustration purposes we show a simplified case, calculated using the model, in which no-motion manifolds are shown in the two-dimensional space defined by the λ s of the jaw closer and opener muscles. The manifolds shown in Figure 4 correspond to static jaw and hyoid configurations which differ only in terms of the jaw orientation angle, α .

The following applies to each of the manifolds shown in the figure. Each manifold consists of λ opener and λ closer combinations for one jaw / hyoid configuration. The different λ pairs, shown with circles, are associated with values of total muscle force which range from 10N to 100N. The solid circles at the right correspond to muscle λ s just sufficient to support the weight of the jaw (the minimum total force at a given position). The total force increases from right to left with open circles showing λ combinations at 10N increments.

In this simplified system, the control underlying movement may be understood as follows: movements may be defined by selecting vectors which produce λ shifts between manifolds, where each manifold comprises the set of jaw and hyoid muscle λ s associated with one

spatial equilibrium configuration. For example, a vector command which opens the jaw from 3 to 6 degrees involves a decrease of the jaw opener λ of about 5 mm and an increase in the jaw closer λ of approximately 2 mm. Muscle co-contraction without motion is also defined by λ shifts, but within a manifold, not between them. In the full jaw model, the idea of λ shifts between and within manifolds is extended to produce four basis vectors which give motion in each of four degrees of freedom and three additional basis vectors associated with muscle co-contraction without motion (the basis vectors of the 3D no-motion manifold).

A central problem in this context is whether, in order to produce movements of a given magnitude in the jaw / hyoid workspace, the system must adjust its commands to take account of musculo-skeletal geometry. The problem is that depending on the position of the jaw and hyoid bone, changes to joint torques arise due to changes to muscle moment arm lengths. Thus when the same command, that is, the same λ shifts, are used in different parts of the workspace, different joint torques and consequently different amplitude movements are produced. Hence the question is how the nervous system takes these changes in musculo-skeletal geometry into account. For instance, is it necessary for the system to maintain an explicit representation of musculo-skeletal geometry to produce jaw movements of some specific magnitude to meet the acoustical requirements of speech?

Using the jaw model, we demonstrated (Laboissière et al., in press) that in spite of a changing muscle geometry, it is possible to define invariant commands involving linear combinations of λ s which produce nearly independent motions in the system's four degrees of freedom from any point in the workspace and give essentially the same movement regardless of the starting configuration of the jaw and hyoid bone. Invariant movement commands were defined as the population mean of individual shortest vectors between

adjacent no-motion manifolds. Commands for co-contraction without motion were orthogonal to the movement commands. Figure 4 demonstrates these ideas in the context of a simplified example of invariant commands for jaw rotation (Λ_α) and co-contraction (Λ_c). We can see that Λ_α is essentially orthogonal to the manifolds in the center of the figure and hence would result in λ change leading to the required rotation alone. Towards the edges of the figure, Λ_α is no longer orthogonal to the no-motion manifolds and, thus, in addition to the intended jaw rotation, a change in co-contraction will be observed. In general, we can see that invariant commands will produce the intended movements along with small yet systematic errors. When using the full model, we have obtained comparable results. Invariant commands resulted in movements of approximately the required magnitudes throughout the jaw / hyoid workspace but they were typically accompanied by small unintended motions in other degrees of freedom (Laboissière et al., in press). This demonstration shows the plausibility of the idea that musculo-skeletal geometry need not be specifically accounted for in movement planning.

Thus we have shown that posture and changes in posture can play an important role in speech movement control. The notion of invariant commands may provide a simple means to achieve this control. The EP hypothesis thus offers a framework in which the relationships between the physical space in speech and its underlying control can be understood. Note, however, that the equilibrium position is, by definition, dependent on all forces acting on the system, and not only on the forces generated by the muscles. Thus, while control may be organized to achieve specific positions in the workspace, the actual equilibrium will depend on gravity and other external forces. For natural speaking conditions, and the usual external loads, it is reasonable to assume that articulatory positions are specified in terms of equilibrium points under the control of λ s.

The Form of Central Commands

Speech targets may exist within our cognitive systems and may be discrete and invariant. These representations must be transformed into the central neural control signals which underlie speech movements. In speech, the form of the control signal is of particular importance as it contributes to our understanding of the relationship between the phonological level and the corresponding organization at the level of the vocal tract. By exploring speech at the level of control, we can assess the extent to which the regularities observed correspond to invariances postulated at the linguistic level. The EP hypothesis, by its very nature, allows us to address the issue of the ways in which the equilibrium as specified at the level of motor system might correspond to aspects of spatial targets, which serve as landmarks in the control of the speech sequence.

Controversies surrounding the notion of targets in speech production have centered on their nature (see e.g., MacNeilage, 1980 for a short review), on their timing (Lindblom et al., 1987 vs. Fowler, 1980), and even on their existence (Pols & Son, 1993). The notion of articulatory targets in speech production is not at all new. It has been used in the debate on speech invariance and variability to support the idea that for a given phoneme, in a given phonetic context, each articulator tends to approach a separate single position (Lindblom, 1963). Figure 5 lets us explore the concept of speech targets in the context of the jaw model. The figure shows empirical and simulated jaw motions during repetitions of [isisa]. The empirical data are shown with dashed lines, the predicted jaw kinematics with solid lines and the presumed underlying equilibrium shifts with dots. The jaw orientation angle is shown in the upper panel and horizontal jaw position is shown below. The data in this figure were obtained using an optoelectronic system. A full description of the

methodology and the data set may be found in Bateson & Ostry (1995).

In fitting the data, we have assumed that the jaw equilibrium angle and equilibrium horizontal position both shift at a constant rate. Changes in the rate and duration of the equilibrium shift are the two controlled variables. Examination of the data shows that the correspondence between empirical and model data is generally good. Note that constant rate equilibrium shifts in the model produce the smooth movements which are observed kinematically. This, of course, is a typical characteristic of muscle systems which act as mechanical low pass filters. Nevertheless, it suggests that simple equilibrium trajectories are sufficient to account for the kinematic details of smooth movements.

The equilibrium shifts, particularly in the case of horizontal jaw translation, are often observed to extend beyond the kinematic endpoints of the movement. The overshoot of the actual trajectory by the equilibrium arises in the model from the need to produce the sufficiently large accelerations which are required to move the jaw in a continuous fashion at rates observed in speech. The need to have the equilibrium position overshoot the actual spatial goal to produce rapid movement has also been demonstrated in simulations of multi-joint arm movements (Hogan, 1985).

The idea that articulatory movements are intended towards spatial positions has been proposed by MacNeilage (1970). However, because the actual articulator position undershoots the equilibrium, our simulations suggest that the literal interpretation of intended equilibrium positions as spatial targets for the articulator may be incorrect. In continuous speech, a combination of continuous equilibrium shifts combined with articulator biomechanical properties creates a situation in which the equilibrium shift must extend beyond the spatial goal. Nevertheless, we think it is reasonable to assume that

regularities relating speech as a linguistic task to speech at the motor level may be found in terms of the control signals as defined by the EP hypothesis. This will, of necessity, entail a comparison of empirical and model data. Regularities relating the units of linguistic description to the control signals of speech motions might be sought in terms of correspondences related to both equilibrium position and rates of equilibrium shift.

The concept of a centrally specified equilibrium or virtual trajectory (Hogan, 1985) may be helpful in understanding the representation of speech targets. However, a variety of different proposals have been made regarding the virtual trajectory form. Whereas Hogan (1985) and Kawato, Maeda, Uno, & Suzuki (1990) have proposed complex virtual trajectories, we have demonstrated above that constant rate equilibrium shifts may underlie jaw movements (also see Flanagan, Ostry, & Feldman (1993) for multi-joint arm movements). The source of the difference between these proposals lies in the modelled physiological and biomechanical properties.

Speech Variability

Variation in articulatory movement is one of the most pervasive characteristics of speech. Some of the aspects of speech movement variability are almost certainly planned, while others may not be planned but may arise from factors such as muscle mechanics, musculo-skeletal geometry and the dynamics of the physical system. Evidence that inter-articulator variations in speech are planned is supported by the findings of Abry and Lallouache (in press, see also Perkell & Matthies, 1992) . These authors analyzed anticipatory lip protrusion in ^{91, (upper case C), 99}[iCy] sequences, in which C represents consonant clusters of 0 to 5 consonants, none of which involved lip protrusion. They showed that the onset time of

the protrusion movement increased linearly with the size of the consonant cluster. The fact that lip protrusion necessary to produce the same final vowel begins earlier in some contexts than in others supports the idea that anticipatory patterns are the result of a process which takes account of upcoming phonetic context when planning successive speech movements.

The kinematic patterns of intra-articulator coarticulation are readily measurable in empirical studies and, on the basis of kinematic changes which arise in response to upcoming phonetic segments, may also appear to be centrally controlled. However, without explicit models of speech articulators, kinematic effects which are correctly attributable to central planning cannot be distinguished from kinematic patterns which are due to dynamics and are not represented in the underlying control. To address this possibility, we present a number of simulations which specifically account for the physical and biomechanical sources of speech variability. We will show how kinematic variability may arise even when the underlying control signals related to the specification of articulatory position remain fixed. The main conclusion we will wish to draw is that unplanned effects due to physical sources must be accounted for before drawing conclusions about central control or inferring planning mechanisms.

Using the jaw model, we have studied the predicted kinematic patterns in simulated V_1CV_2 transitions. In these simulations, the equilibrium shifts associated with the V_1C movement remain constant in duration and in amplitude while the equilibrium shifts associated with the CV_2 movement are varied in amplitude and constant in duration. The different amplitudes of CV_2 shifts simulate observed differences in jaw position and orientation for different final vowels (Ostry & Gracco, 1995). The co-contraction level in these simulations was constant throughout. Thus, at the level of central control, no

account was taken of upcoming context in the specification of the V_1C transition. However, when one examines the predicted kinematic patterns (Figure 6), we see that the V_1C amplitude and duration are systematically affected by the identity of the final vowel. As movement amplitude for the final vowel decreases, the simulated amplitude and duration of the initial transition increase. Comparable patterns of intra-articulator coarticulation have been reported in empirical studies of jaw, tongue dorsum, velar, and lower pharyngeal wall coarticulation (Ostry & Gracco, 1995; Parush, Ostry, & Munhall, 1983; Parush & Ostry, 1986; Parush & Ostry, 1993). Thus, while on the basis of kinematic evidence alone, it could be concluded that intra-articulator coarticulation is consistent with the notion of planned coarticulation, our present simulations suggest that this possibility be evaluated with care. The issue we wish to raise with this simulation is not whether there is actually adjustment for context but rather, that unless we are able to separate the effects of dynamics from those of central control, the issue cannot be resolved.

Kinematic variability may also arise from a combination of the co-contraction level and dynamics, even when the equilibrium shift which underlies the movement remains constant. Figure 8 shows results of simulations in which 5 mm equilibrium shifts at the mandibular incisors are produced in each of eight directions (see Figure 7). Each of the equilibrium shifts from the central position to one of the eight target positions (and back again) occurred at a constant rate and was 300 ms in total duration. Twenty different levels of co-contraction were tested at each movement direction. Two kinds of variability may be seen in the figure. The simulated jaw incisor trajectories differ depending on movement direction. This is a result of particular interactions in the model between the dynamics of jaw rotation and translation. The trajectories also vary for each specific direction of equilibrium shift. This is due to differences in the level of co-contraction. The overall

variation in final movement extent for different movement directions is given in the lower panel. Directional error is not shown. It should be noted that the least variable among this set of simulations are those in the directions corresponding to actual jaw movements in speech.

Variation in endpoint position may also occur when invariant commands are used (described above). Figure 9 uses invariant commands to assess in statics the variability of final jaw position at the mandibular incisors for 5 mm equilibrium shifts in different directions. Differences due to dynamics are not shown. Variations in both movement amplitude and direction may be observed. The lower panel shows the error in movement extent only. The different final jaw positions arise in the simulation as a result of different initial distributions of muscle force at the same initial starting position. In other words, when invariant commands are used, the final position depends on the point on the no-motion manifold from which the movement begins. Thus overall, our simulations suggest that even in situations where the extent of equilibrium shift is fixed, variation may arise due to dynamics, due to the combination of the co-contraction level and dynamics, and due to use of invariant commands.

DISCUSSION

In this paper, we have described a model of jaw and hyoid motion based on the EP hypothesis. We have shown that this hypothesis permits a description of the relation between vocal tract geometry and the physiological control underlying motion. We have described simulations which examine the form of the central control signals. We have shown that smoothness in movement may arise from dynamics and need not be planned.

We have suggested that regularities relating speech as a linguistic task to speech at the motor level may be found in the control signals underlying movement. We have examined a number of sources of articulatory variability. We have shown that kinematic patterns comparable to those reported in intra-articulator coarticulation may arise as a result of dynamics rather than central planning. We have also shown that trial-to-trial variation may occur with a fixed movement command in cases where the movements occur with different levels of co-contraction.

A number of formal models of the speech articulators have been proposed which focus primarily on aspects of articulator and vocal tract geometry (Harshman, Ladefoged, & Goldstein, 1977; Mermelstein, 1973; Maeda, 1990). There exist as well formal models which focus on the biomechanical characteristics of tongue and laryngeal motion (Kiritani, Miyawaki, & Fujimura, 1976; Perkell, 1974; Wilhelms-Tricarico, 1995). We know of relatively few formal models which focus on speech control directly (Browman & Goldstein, 1985; Lindblom, 1967; Saltzman, 1986; Saltzman & Munhall, 1989). We will contrast the approaches to speech control with the approach we have taken in the present paper.

Lindblom (1967) presented a simplified model of jaw motion in which the underlying motor commands involved the control of force. He suggested that movements are represented in terms of targets which are associated with specific levels of force. The model was able to successfully predict duration differences between closed and open vowels. However, a weakness of the model is the choice of the control variable. It should be recognized that force is a dependent variable rather than one which is independently controlled. As shown in Figure 1, the same level of force can be associated with different muscle lengths (for example, points (b) and (c) in the panel at the lower right). Hence, the control of force cannot lead to the specification of unique positions. In addition, the force requirements to

reach a given final position in the space will vary with the actual position of the articulator. Thus, some alternative other than force control must account for the achievement of final position.

Saltzman (1986) reported a model relating vocal tract variables such as constriction location and constriction degree to articulatory variables for the jaw, tongue, lips and glottis. In the model, targets are defined as attractors in the space of vocal tract variables. The model is able to generate smooth movement trajectories and synthetic speech. It successfully accounts for phenomena such as lip / jaw compensation in response to perturbation and syllable reduction with increases in speaking rate (Browman & Goldstein, 1990). The model is comparable to one presented in the present paper to the extent that movements in the Saltzman model arises from changes in the equilibrium state. However, a number of differences may be noted. Control in the Saltzman model is effectively abstract: There is no physiological mechanism underlying the control. In addition, the position of each articulator is inferred from a trajectory towards an attractor in the task space. The dynamic behavior of each articulator is therefore dependent on properties of the dynamic attractor in the task space. No account is given of either the inertial properties or the muscle mechanical properties of the articulator.

The λ model was originally developed in the context of human arm movement. We now consider the appropriateness of the model in the context of speech. The issue of particular importance concerns the availability in jaw and hyoid muscles and other tissues of sources of afferent facilitation to MNs (see Hannam & McMillan, 1994; Lund, Lamarre, Lavigne, & Duquet, 1983; Luschei & Goldberg, 1981; Rowlerson, 1990; Smith, 1992 for reviews) Recall that the model suggests that afferent facilitation associated with muscle length and velocity sum with direct central facilitation to α MNs. Muscle spindle receptors may

provide this information in jaw closer muscles such as masseter and temporalis. However, while there are some spindles in the jaw opener anterior digastric, their number is very few in comparison to the closer muscles. Nevertheless, both an unloading reflex and a small amplitude tonic stretch response have been recorded in human jaw opener muscles (Hannam, Matthews, & Yemm, 1968; Lamarre & Lund, 1975; Neilson, Andrews, Guitar, & Quinn, 1979). In addition, we have recently recorded both tonic and phasic stretch responses in jaw opener muscles in four subjects (unpublished observations). These demonstrations are consistent with the possibility that afferent facilitation to jaw opener MNs may arise directly from jaw opener afferents (including non-spindle afferents). The presence of a tonic vibration reflex in jaw openers (Hellsing, 1977) indicates that facilitation also arise from mechanoreceptors, perhaps those associated with the temporomandibular joint and its ligaments. Moreover, in the rat, there are reflex connections between jaw closer muscles and jaw opener MNs which may also provide afferent facilitation (van Willigen, Juch, Ballintijn, & Broekhuijsen, 1986). In short, while afferent facilitation to jaw opener MNs may arise to only a limited extent from direct spindle afferent input, there are sufficient alternate sources of facilitation. Thus, the application of the EP hypothesis to the control of speech articulators seems entirely appropriate.

Acknowledgements

This research was supported by the European Union (ESPRIT-BR Project No. 6975), NIH grant DC- 00594 from the National Institute on Deafness and Other Communication Disorders, NSERC-Canada, FCAR-Québec, Coopération France-Québec, and Région Rhône-Alpes.

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Appendix

This appendix outlines the basic structure of the model. For a detailed presentation of the jaw model see Laboissière, Ostry, & Feldman (in press).

The model suggests that neural control signals specify muscle threshold lengths (λ) through changes to MN membrane potentials (Feldman, Adamovich, Ostry, & Flanagan, 1990). Muscle activation, A , is dependent upon the difference between the current muscle length, l , and λ as well as on the rate of muscle length change, such that:

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

where

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

The parameter μ which is positive in value specifies the dependence of the muscle's threshold length on velocity and provides damping due to proprioceptive feedback. Damping due to muscle intrinsic properties such as the muscle's force-velocity relationship is also included in the model.

Muscle length and velocity dependent reflex delays are likewise included. After taking into account a time varying central command and a reflex delay of d ms, muscle activation, $A(t)$ becomes:

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

A reflex delay, d , of 10 ms has been used for all muscles. The value was based on observed delays in jaw closer unloading responses in humans and monkeys (Luschei & Goldberg, 1981; Lamarre & Lund, 1975).

Changes to λ and hence to muscle activation are associated with MN recruitment and increases in MN firing rates. The resulting dependence of active force, M , on the difference between the actual and threshold muscle lengths is approximated by an exponential function of the form:

$$M = \rho \exp(cA) - 1, \quad (4)$$

where c is a form parameter and ρ is a magnitude parameter whose value varies with the force generating capability of the muscle (see Laboissière, Ostry, & Feldman, in press concerning the estimation of these parameters and the sources of the parameter estimates). It should be noted that the exponential dependence of force on muscle length is consistent with the size principle (Henneman, Somjen, & Carpenter, 1965). As the difference between the actual and threshold muscle length increases, progressively larger motor units are recruited and larger increments in force are observed.

A number of features of the model should be noted. Position and velocity dependent reflex inputs provide facilitation to homonymous α MNs. Reflex inputs to synergists are not modeled. As there is no Ia inhibitory interneuron between either closer or opener muscle groups nor Renshaw inhibition in jaw muscles (see Olsson & Landgren, 1990 for review), neither is represented in the model (see Feldman, Adamovich, Ostry, & Flanagan (1990) for the effects of reciprocal inhibition in a model of arm motion based on the λ model.).

Comparable reciprocal patterns of central origin — hyperpolarization of jaw closer MNs

during jaw opening (Goldberg & Tal, 1978) — have not been modeled.

Note as well, that the effects of specific discharge patterns in MNs and spindle afferents (patterns of spike-like activity) are both realized in the model in terms of their effects on the membrane potentials of MNs. However, individual spike trains which may be measured electrophysiologically have not been modeled directly. Similarly, the specification of the parameter, λ is not discrete. The model assumes there is continuous variation in central commands, resulting in a time varying shift in the threshold muscle length for MN recruitment.

Spatial and temporal control may vary independently. By changing the rate and duration of λ shift temporal and spatial variation in articular motion are achieved. However, the model imposes no special constraints on how central commands can evolve in time. Hence both the timing and position patterns of articulators in speech can be predicted.

FIGURE TITLES

Figure 1. Jaw configurations (left hand panel), levels of MN depolarization (upper right) and jaw muscle force-length curves (lower right) (see text for details).

Figure 2. The muscle λ s and the corresponding torque-angle curves are shown in the right hand panel for a simplified jaw system involving a single closer muscle and a single opener muscle (left hand panel). The equilibrium angle, α , is the angle at which jaw closer and jaw opener torques are balanced. Central commands can change alpha and the level of co-contraction independently by shifting λ_c and λ_o in the same direction or the opposite direction, respectively. The sum of the muscle torque-angle curves (labelled total torque) gives the torque-angle curve for the joint. The slope of this function represents jaw stiffness.

Figure 3. Schematic representation of the jaw model and the modelled muscles. The upper panel gives the overall layout of the model including the central control signals, modelled muscles, dynamics and afferent feedback. The representation of each individual muscle is shown in the lower panel (see text for details).

Figure 4. No-motion manifolds (jaw opener and jaw closer λ combinations for different total force levels at various jaw orientation angles, α). The solid circles at the right of each manifold correspond to the point of minimum total force for that jaw configuration. λ combinations associated with higher total force levels (shown at 10 N increments) are represented by the open circles on each manifold. Control signals associated with changes in the jaw equilibrium angle α can be defined in terms of vectors between manifolds. Changes to the co-contraction level are produced by changing the magnitude of a co-contraction vector which is orthogonal to the vector producing motion.

Figure 5. Empirical and model data during repetitions of [isisa]. The hyoid bone is at the assumed rest position for occlusion during the simulated movement. Empirical data are shown with dashed lines (see Bateson & Ostry (1995) for details); simulation results are shown with solid lines; dotted lines show central commands. In each phase of the movement the central commands for rotation and translation commands start and stop at the same time. The co-contraction is fixed. The fit was done by hand; a quantitative evaluation of the goodness of fit was not carried out.

Figure 6. Predicted kinematic patterns (solid lines) of jaw rotation (above) and horizontal jaw translation (below) and the presumed underlying control signals (dashed lines) during a V_1CV_2 utterance. Note that whereas the magnitude and the duration of the equilibrium shifts associated with the V_1C transition are fixed, the predicted V_1C duration and movement amplitude vary with V_2 .

Figure 7. Sources of variability in jaw motion are explored in the context of equilibrium shifts of the mandibular incisors in eight different directions (see text).

Figure 8. Variability associated with 5 mm equilibrium shifts in each of the eight directions shown in Figure 7. The equilibrium shifts used here are fixed in rate, magnitude and direction. As exact λ commands were used in the simulations, the variation only arises from different levels of co-contraction and interactions in the model between jaw rotation and translation dynamics. Each path corresponds to a given level of co-contraction on the no-motion manifold, meaning different levels of total muscle force (ranging from 20 to 70 N). The lower panel gives the mean extent and standard deviation of the simulated movement in each of the eight directions tested.

Figure 9. Variability in statics arising from the use of invariant commands (see text and

Figure 8). For each of the eight directions shown in Figure 7, mean final position error and standard deviation in each direction are presented in the lower panel.

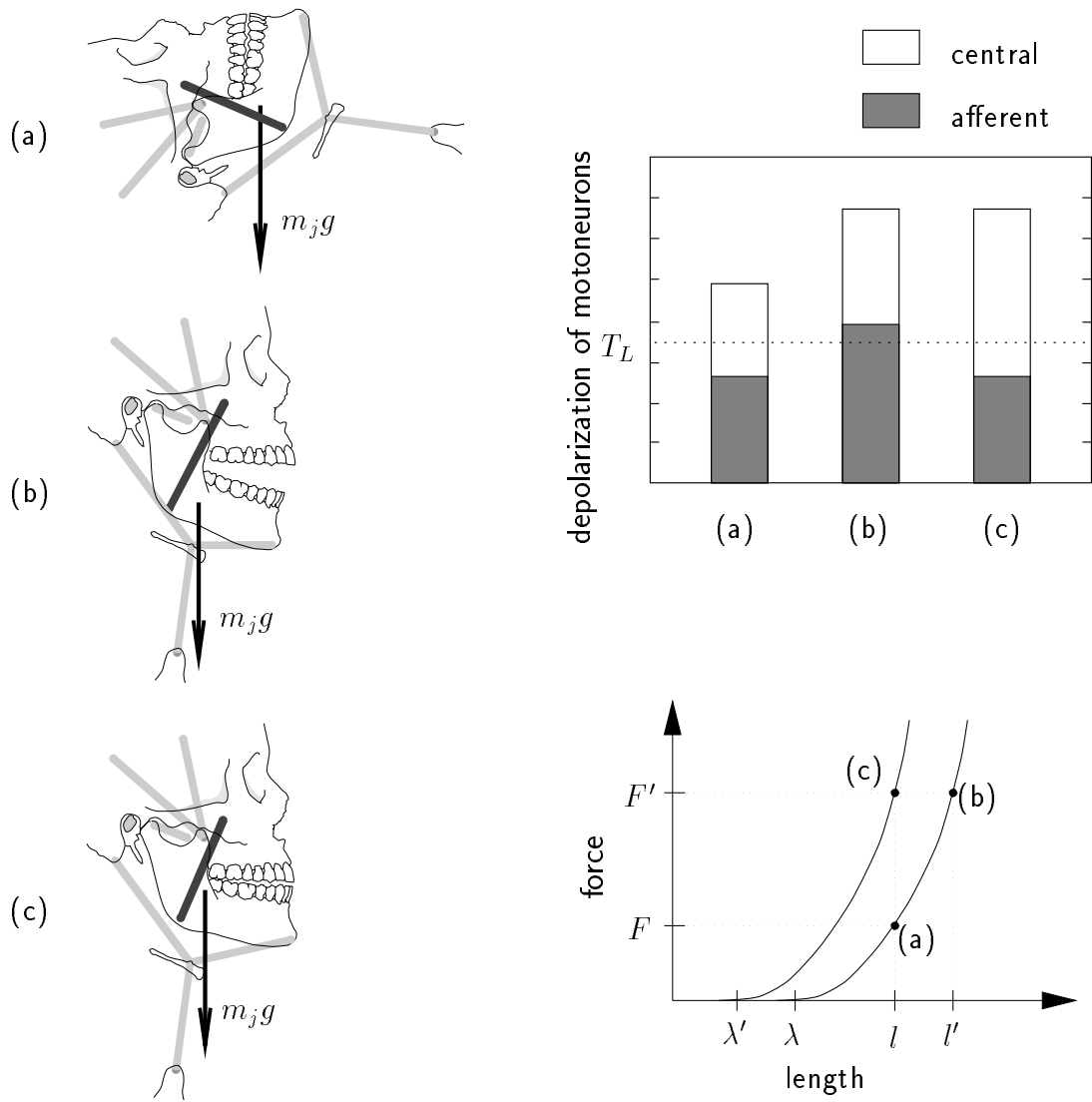


Figure 1:

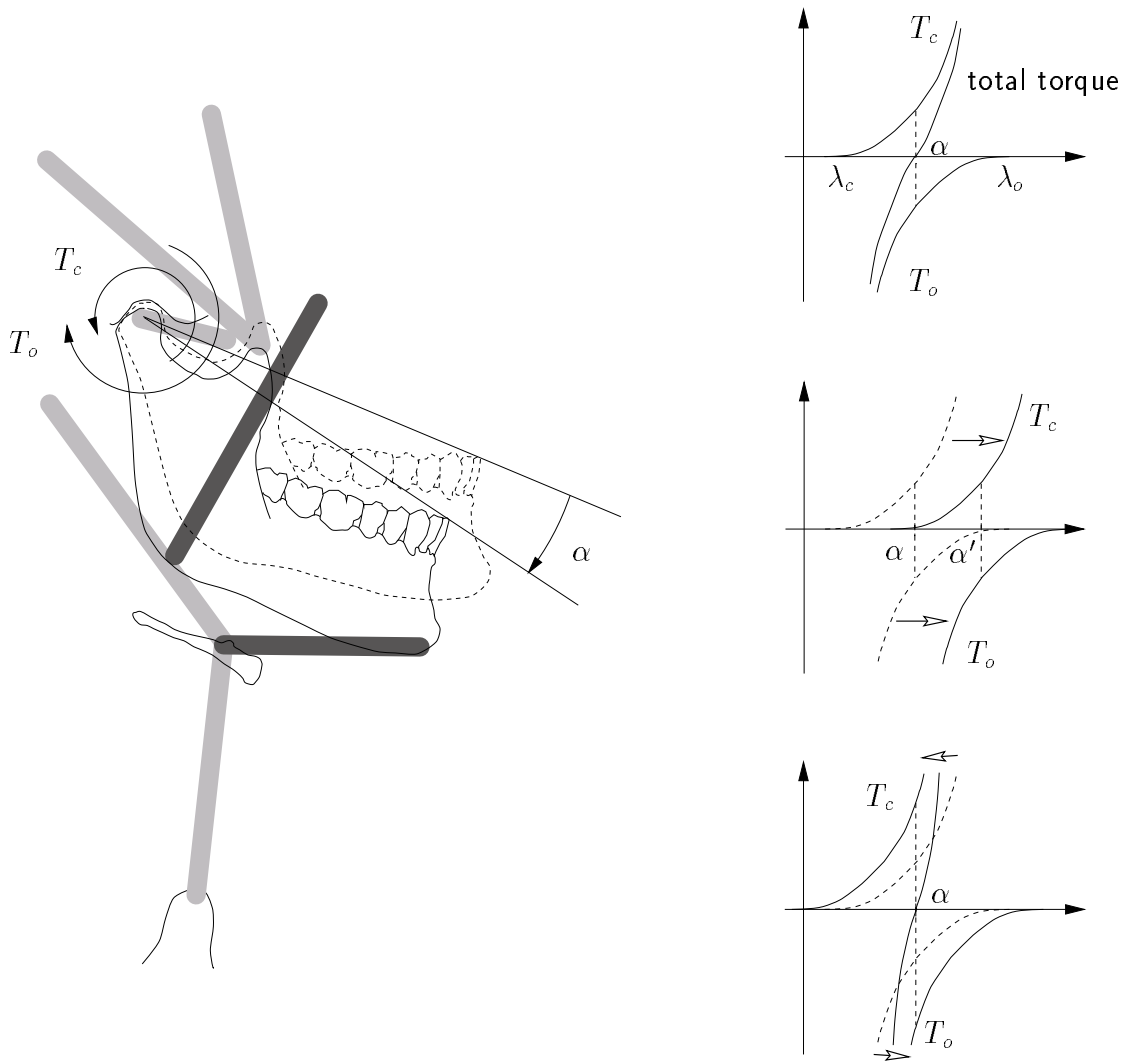


Figure 2:

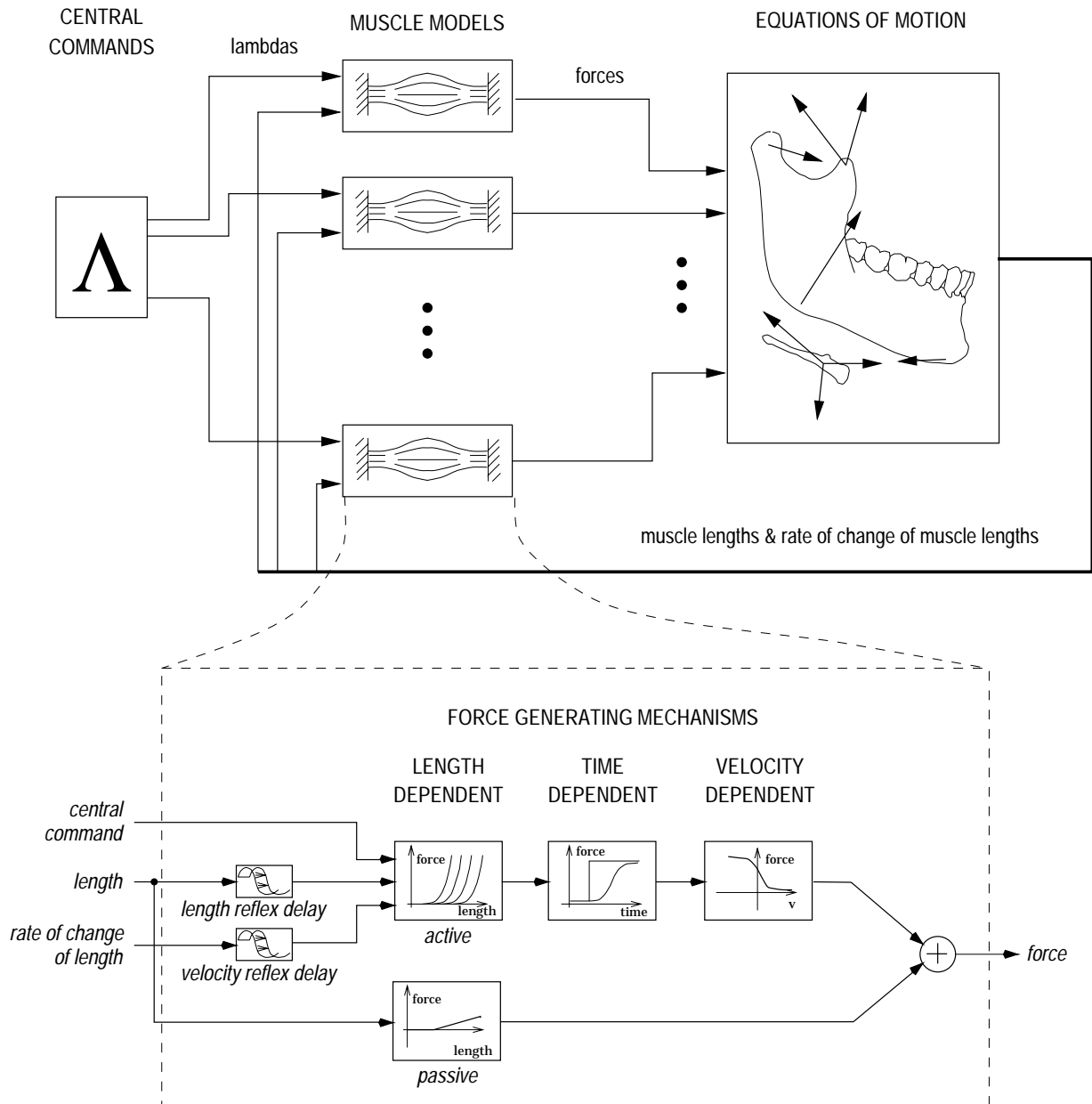


Figure 3:

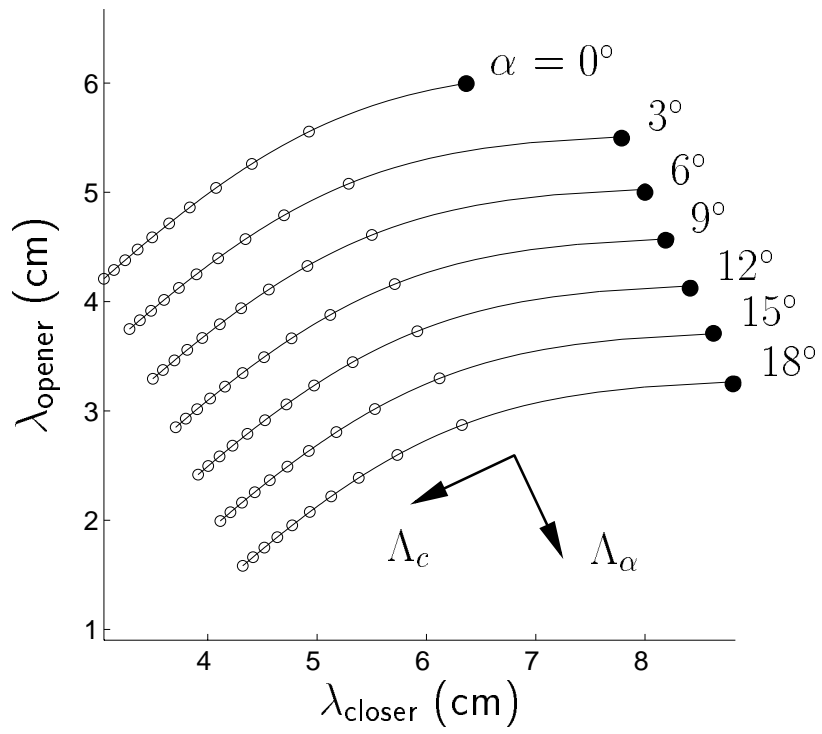


Figure 4:

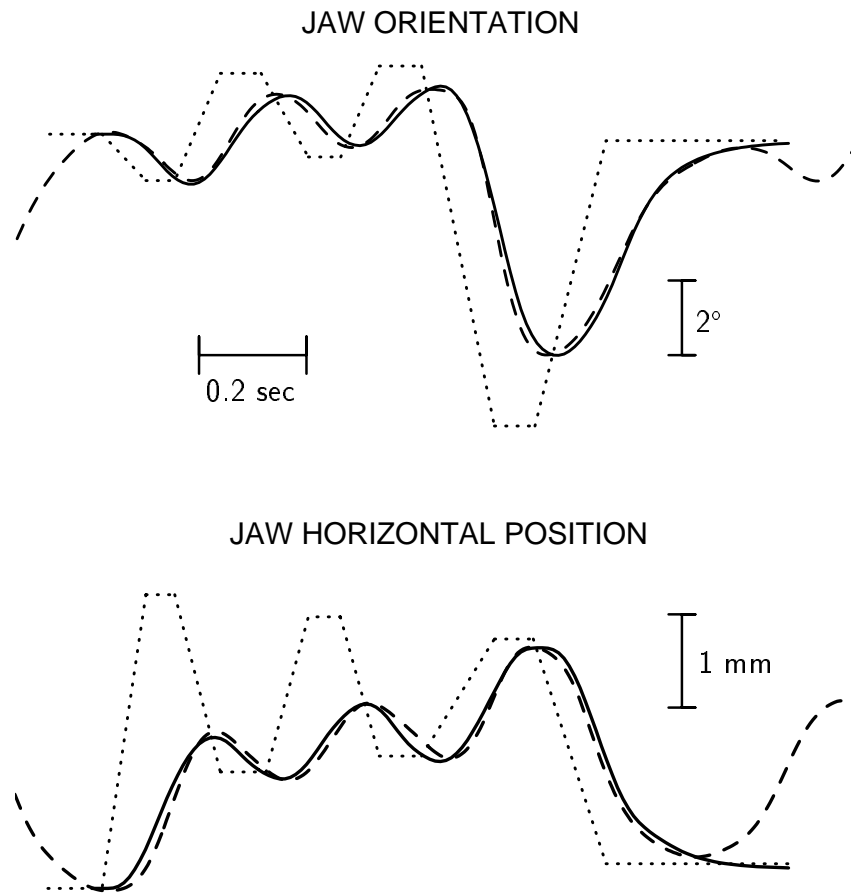


Figure 5:

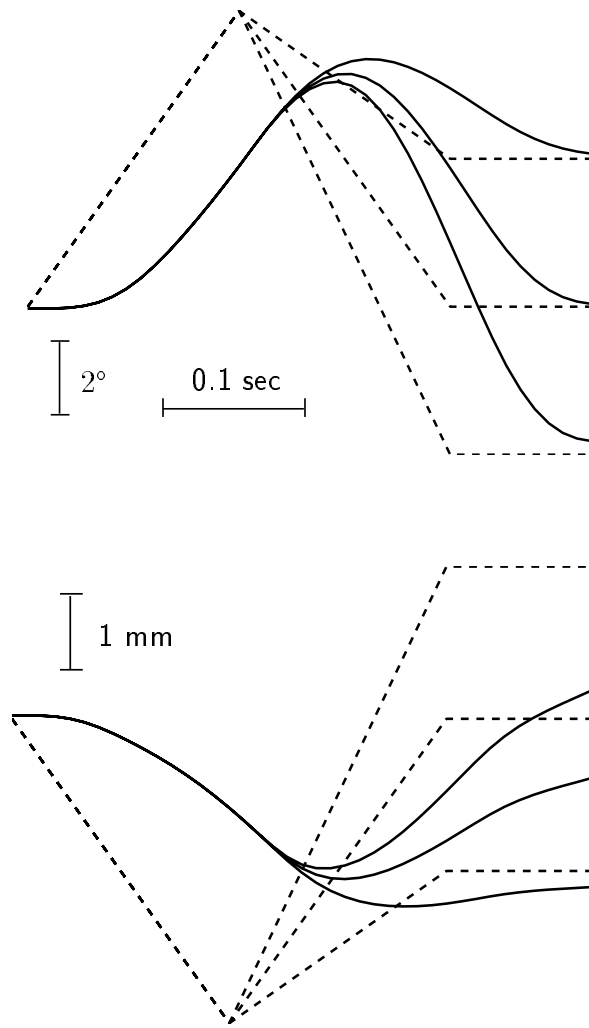


Figure 6:

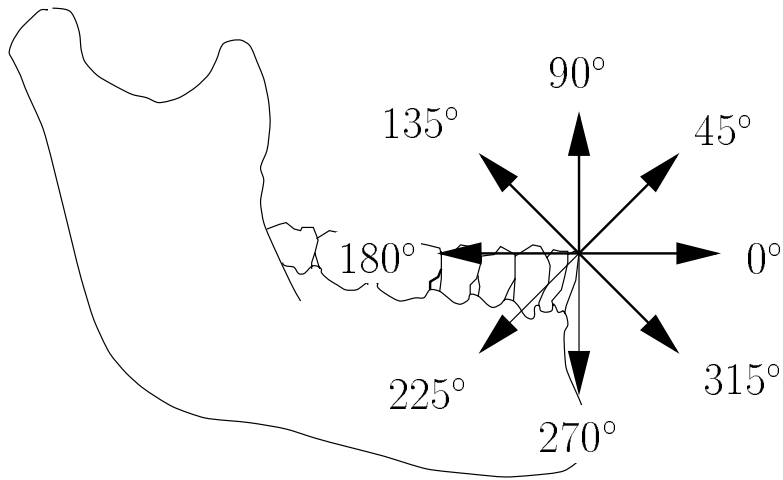


Figure 7:

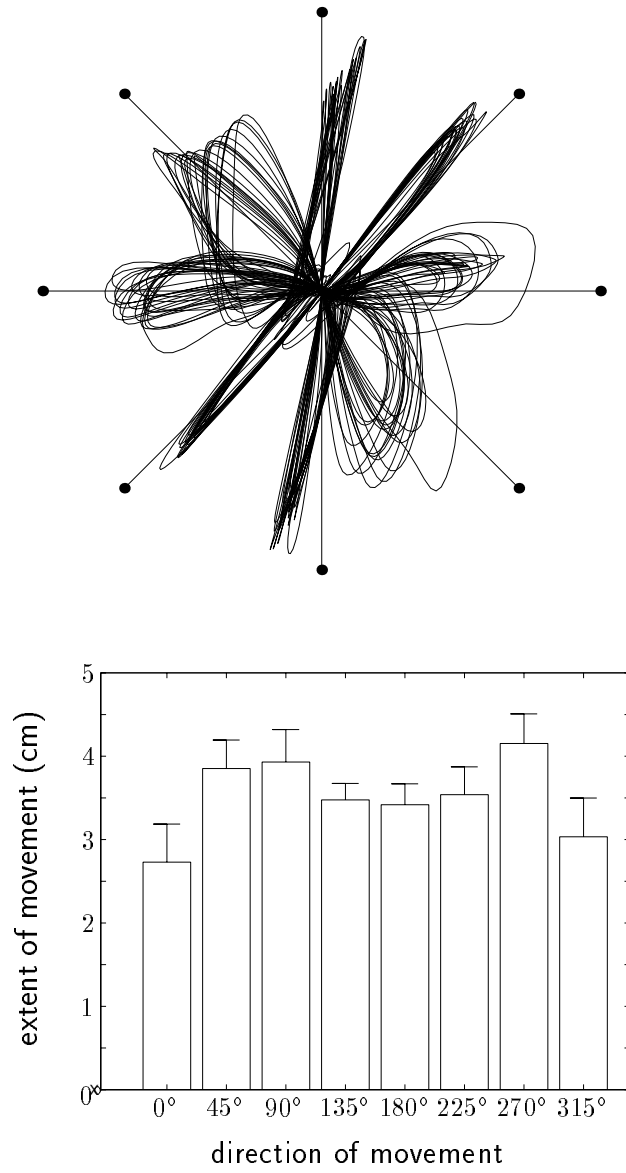


Figure 8:

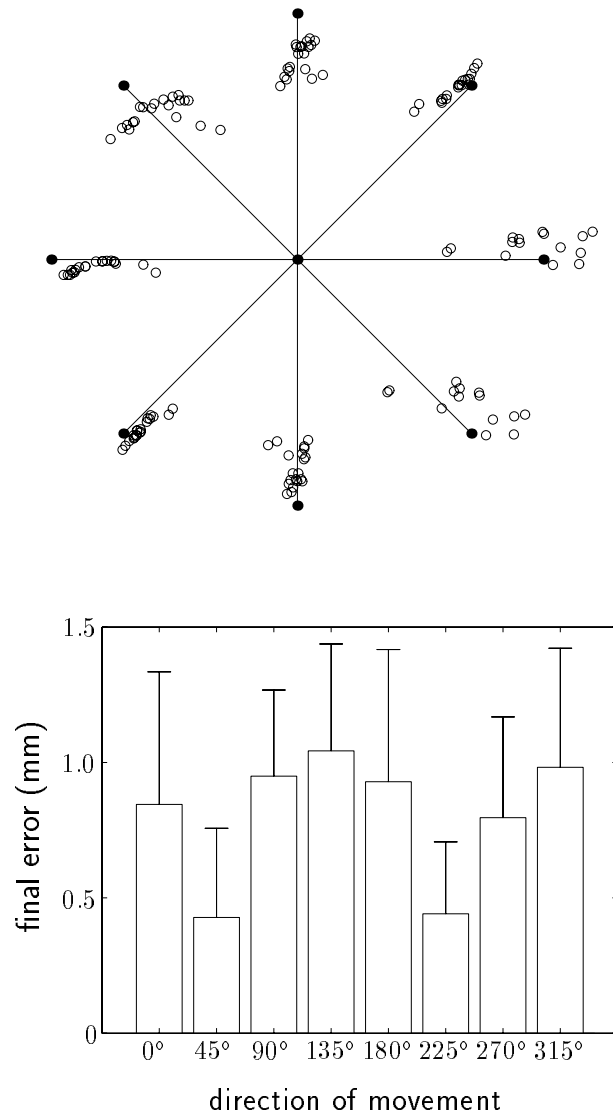


Figure 9: