

Chapter 4

SENSORIMOTOR MECHANISMS IN SPEECH MOTOR CONTROL

Vincent L. Gracco

A conceptual model of speech motor control is developed in which the elemental units for speech are sound-producing coordinated movements of the vocal tract. The perspective taken is that the degrees of control freedom are at a systems level; in the operation of the processes that implement the speech motor action. Speech motor control is conceptualized as a multistage parallel process in which vocal tract specifications are activated by central motor commands which interact with a central rhythmic output to produce serial coordinated movements that generate sound. Vocal tract specifications include the selection of characteristic neuromotor patterns, which map isomorphically onto the phonemes of the language. Coordination of the contributing movements and on-line spatial adjustments within and among vocal tract structures are inherent in the neuromotor patterning and activation processes, respectively. The elemental units are retrievable elements stored in the central nervous system and instantiated by the directed action of the posterior parietal cortex. Two major brain systems (basal ganglia-supplementary motor area and the cerebellar-premotor) are proposed to play major roles in implementing neuromotor specifications by modulating the characteristic patterns and the sequencing their actions into larger meaningful units of production. It is the action and interaction of these sensorimotor mechanisms that result in the speech motor patterns characteristic of human verbal communication.

INTRODUCTION

"If you root yourself in the ground, you can afford to be stupid. But if you move, you must have mechanisms for moving, and mechanisms to ensure that the movement is not utterly arbitrary and independent of what is going on outside."

Patricia Smith Churchland 1986.

After years of theoretical debate and endless empirical investigations, the classic central-peripheral issue that has guided much of the research in motor theory has given way to the more reasonable perspective that movement reflects an interaction of peripheral influences and central motor processes; behavior is sensorimotor in nature. Moreover, it is becoming increasingly clear that any behavior is a reflection of multiple overlapping and interacting influences, each of which needs to be identified. The purpose of identifying the subcomponents is not

strictly to assign function to structure but to evaluate their potential contribution to the overall process, and hence allow development of realistic and biologically plausible working models of the system. An important research focus in human motor behavior has become the development of models that capture the essence of sensorimotor control (P. M. Churchland, 1989; McClelland & Rumelhart, 1986; Marr, 1982; Pellionisz & Llinas, 1979; Pellionisz & Llinas, 1985; Rumelhart & McClelland, 1986). The rationale for such an endeavor is two fold: first, there is an inherent richness and intricacy to even the simplest problem of sensorimotor control, and second, there is an implicit assumption that higher functions such as cognition are not discontinuous with the lower level sensorimotor functions that implement them (see P.S. Churchland). In this regard a statement by Hughlings Jackson made over 115 years ago seems prophetic:

"I cannot conceive what even the highest nervous centres can possibly be, except developments out of lower nervous centres, which no one doubts to represent impressions and movements."
J. Hughlings Jackson 1875.

Because of its well-learned and ethologically significant nature, speech is an ideal behavior for the investigation of sensorimotor control mechanisms. Moreover, as a reflection of one of man's most highly developed behaviors, a thorough understanding of the processes of communication may provide invaluable insight into the operation and functional organization of the human nervous system.

The purpose of the following chapter is to propose a preliminary conceptual model of speech production from a functional (e.g., communicative) perspective that is grounded as much as possible in physiological mechanisms and plausible nervous system processes. Implicit in any model of human behavior is the tacit assumption that the hypothetical processes or functions actually exist in some form in the central nervous system or at least emerge from central, peripheral and/or biomechanical interactions. As such, the conceptual model will be limited to constructs known or suspected from nervous system mechanisms. How many different mechanisms are required to explain the observable behavior? What aspects of the observable behavior need to be explained or accounted for? What role does peripheral sensory information play in the control of speech movements? What are the organizational principles for speech production? These are some of the issues that will be dealt with in the following chapter. Because the model presented is conceptual in nature and preliminary in form, only basic principles will be presented and many details will be lacking. One important component that will not be discussed is the contribution of the biomechanical periphery to the shaping of the complex kinematic patterns characteristic of speech. Only through incorporation of the physical properties of the vocal tract with underlying sensorimotor mechanisms can a realistic and parsimonious model be constructed. Within this limitation, a focus on underlying global sensorimotor processes should provide an additional and potentially viable perspective on speech production and perhaps a better perspective on motor speech disorders as well.

ORGANIZATIONAL STRUCTURE FOR SPEECH MOTOR CONTROL

In order to discuss the sensorimotor mechanisms that may underlie speech production it is first necessary to determine the most plausible conceptualization of the system being controlled. During speech, different vocal tract actions are sequenced to produce groups of linguistically-relevant sounds. Over the last 8-10 years, attempts have been made to determine the specific organization for speech motor control, i.e., to identify the appropriate level of articulatory organization. The lack of invariant individual articulatory actions and the relatively consistent ensemble articulatory actions suggests that the nervous system does not explicitly control the action of a single muscle or articulator (Kelso & Tuller, 1984; Gracco & Abbs, 1986; Saltzman, 1986). Rather, speech motor actions are organized at a level that reflects the interaction of a number of muscles and/or articulators engaged in the same functional task. For example, the final positions of the upper lip, lower lip, and jaw during bilabial production are not invariantly attained but vary systematically within some limit such that an apparent goal, oral closure, is achieved (Gracco & Abbs, 1986). Similarly, when the movement of an articulator is unexpectedly impeded during its normal motion, displacement is increased in the perturbed articulator as well as in various unperturbed articulators actively involved in producing the movement goal (Abbs & Gracco, 1984; Gracco & Abbs, 1985; 1988; Kelso et al., 1984; Shaiman, 1989). Relative timing patterns observed for the upper lip, lower lip, jaw, and lower lip, jaw, and larynx in various phonetic contexts suggests that coordinative adjustments across vocal tract components is an important property of the motor control process (Gracco & Löfqvist, 1989; Gracco, 1988; Gracco & Abbs, 1986; Löfqvist & Yoshioka, 1981; 1984). Consistent relative timing relations, distributed compensatory actions, and systematically variable articulatory interactions suggest that speech motor control must be viewed from a perspective encompassing ensemble articulatory actions. An important research question is the size of the ensemble, i.e., the size of the production unit.

One possible approach to the question of articulatory organization is captured in the construct of a coordinative structure (Fowler, Rubin, Remez & Turvey, 1980; Kelso, 1986; Kugler et al., 1980; Saltzman & Kelso, 1987; Turvey, 1977). For speech, such a style of organization involves a number of flexible, but relatively constrained articulatory actions or ensembles, represented conceptually as tract variables (see Saltzman, 1986; Saltzman & Munhall, 1989) or physiologically as functional synergies (Fowler et al., 1980; Kelso, 1986; Kelso & Tuller, 1984) assembled into larger action units to produce sound (Browman & Goldstein, 1989; 1990; Saltzman, 1986; Saltzman & Munhall, 1989). From this perspective, speech sounds result from the assembly of vocal tract actions (constriction producing events) from presumably independent primitive gestural units (Browman & Goldstein, 1989; Fowler et al., 1980; Kelso, 1986). This particular organizational scheme can be thought of as horizontal in the sense that the vocal tract is partitioned into articulatory subsystems which are marshalled into task-specific

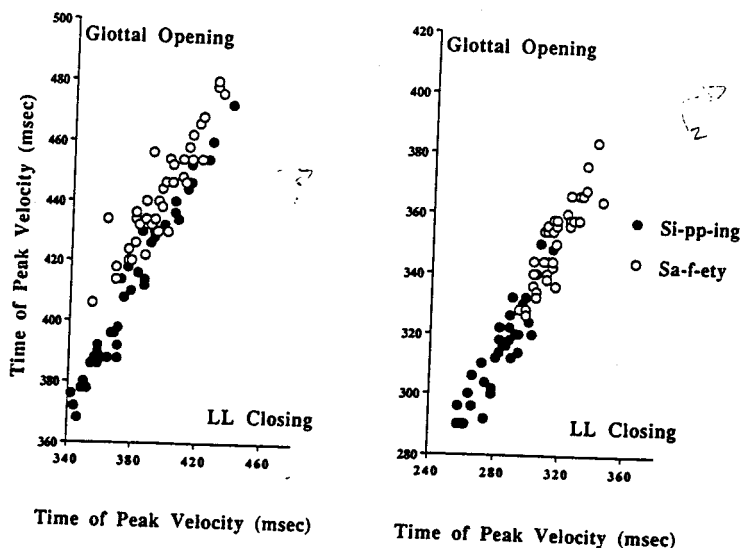


Figure 1. Scatterplots of the relative timing of lower lip peak velocity and the glottal devoicing peak velocity for occlusion /p/ (filled circles) and frication /f/ (open circles) for two subjects. For both subjects the relative timing of the articulatory events is constrained and similar across manner of production.

patterns (Kelso, 1986). However, one assumption of the coordinative structure, i.e., an active process that pieces together or assembles elementary or primitive articulatory actions has never been critically evaluated.

The construction of complex behaviors from simpler movements has been suggested for other tasks such as locomotion (Flashner, Beuter, & Arabyan, 1988), handwriting (Hollerbach, 1981; Morasso & Mussa-Ivaldi, 1982; Edelman & Flash, 1987; Lacquaniti, 1989) and pointing movements (Atkeson & Hollerbach, 1985; Morasso, 1981). A major difference, however, is that the behavior is organized vertically in the sense that complex behavioral sequences are composed of a smaller segments involving the entire effector unit rather than anatomical parts. For example, a primitive stroke in handwriting would involve all necessary components of the shoulder, arm and hand to produce a curved line (an elemental stroke) rather than isolated actions of the parts. Using the same analogy, speech production may be described as the concatenation of fundamental actions such as opening the vocal tract (as in the production of vowels) and closing the tract (as in the production of consonants) which produce or modulate sound. Rather than viewing the production of a /p/, for example, as involving a number of independent gestures (lip aperture gesture, a glottal gesture, an oral and pharyngeal gesture, and a velar gesture) assembled through a coordinative process, a simpler perspective is to view speech production in a wholistic sense in which characteristic neuromotor patterns, involving all components of the vocal

tract, is the elemental control structure for speech. It can be argued that observations of distributed compensatory actions involving local and remote articulatory adjustments (Abbs & Gracco, 1984; Folkins & Abbs, 1975; Folkins & Zimmermann, 1982; Gracco & Abbs, 1988; Kelso, Tuller, V.-Bateson & Fowler, 1984; Shaiman, 1989) are consistent with a level of organization in which vocal tract configurations are manipulated with no need for additional processes to assemble fundamental, nonspeech producing units. Similarly, recent findings such as the apparent adjustment in laryngeal timing to lower lip perturbation (Munhall & Löfqvist, 1986) and the consistent relative timing among lip constriction/occlusion movements and glottal devoicing (see Figure 1 from Gracco & Löfqvist, 1989) suggest that neuromuscular adjustments across vocal tract structures are accomplished through manipulation of a common driving signal (Gracco, 1988) applied in a systematic manner to all active components of the vocal tract involved in producing a particular sound. It is apparent, however, that the available empirical evidence is consistent with either perspective and that conceptual identification of "the" primitive units of speech motor control is not important. Only in attempting to develop a realistic and parsimonious neurobiological and biophysical model of speech motor control does this issue have direct theoretical relevance.

CHARACTERISTIC MOTOR PATTERNS

As suggested above, coordinated sound-producing vocal tract actions, consistent with a segmental organization, are viewed as the smallest functioning structural units in the sensorimotor control process for speech. These hypothesized units are not abstractions, but characteristic neuromotor patterns whose implementation result in the production of sound. The characteristic patterns are similar to ideas presented by others such as Joos (1948), Fowler (1983), Saltzman & Munhall (1989) and Löfqvist (1990) but differ mainly in their level of description. At a neurophysiological level, these characteristic patterns are not invariant but are hypothesized to reflect a reference neural substrate which other sensorimotor processes act on resulting in output variability. This conceptualization is different from earlier speech production models which postulated the presence of invariant motor commands in that the patterns are one part of a distributed process, not the output of the system. The suggestion that speech production involves characteristic (not invariant) patterns is both logical and observable. For example, bilabial production always involves, to some degree, the same muscles produced with related characteristic actions. For example, presented in Figure 2a and 2b is a representative neuromuscular pattern for the upper and lower lip muscles and the resulting movement for the nonsense word "sapapple". Within certain boundary conditions, oral opening for an open vowel for /ae/ will result in some activity in upper lip and lower lip elevator and depressor muscles, respectively indicated in the figure (Figure 2a) by levator labii superior (LLS) and depressor labii inferior (DLI) (Figure 2b). Oral closing for any bilabial will involve some degree of activity in upper lip depressor muscles such as depressor anguli oris (DAO) and

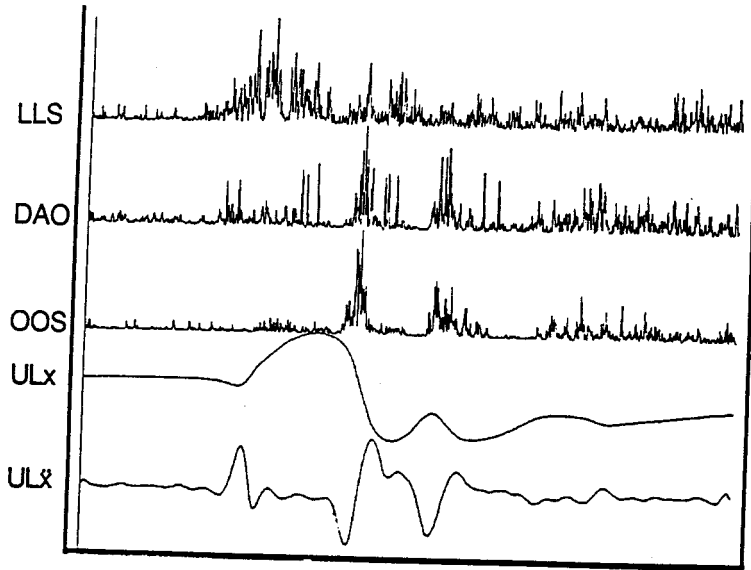


Figure 2a. Rectified muscle activity for an upper lip elevator (levator labii superior, LLS), two upper lip depressors (depressor anguli oris, DAO, and orbicularis oris superior, OOS), upper lip displacement (ULx) and acceleration (bottom trace) illustrating a portion of what can be considered a neuromuscular pattern for oral closing. For the upper lip, the large negative-going acceleration marks the onset of the segment, followed by phasic bursts of muscle activity in DAO and OOS accompanying the oral closing.

orbicularis oris superior (OOS) (Figure 2a), and activity in lower lip elevators (Figure 2b) such as mentalis (MTL) and orbicularis oris inferior (OOI); some cocontraction in LLS and DLI will accompany the closing action presumably to increase the overall stiffness of the lips and/or perhaps to damp the movements. This description reflects a consistent pattern of muscle action that accompanies all bilabial sounds. In contrast, bilabials are not produced with the tongue and, all things equal, are usually produced at a faster rate than vowel sounds. While there are certainly differences in some of the other contributing muscles in the vocal tract depending on whether the sound is /p/, /b/, or /m/, these are based on the particular aerodynamic or acoustic requirements for the sound. Similarly, the relative timing of such actions are also systematically related indicating that while the timing patterns may differ, they are related in a predictable manner observing simple scaling laws (Gracco, submitted). What uniquely defines each sound in the language is its particular neuromuscular configuration reflecting a distinct spatio-temporal pattern of activation and resulting motion. These patterns are not designed to explain all the details of observable speech movement actions, but are viewed as one fundamental component in the motor control process. Each component or group of components in the specification may have different

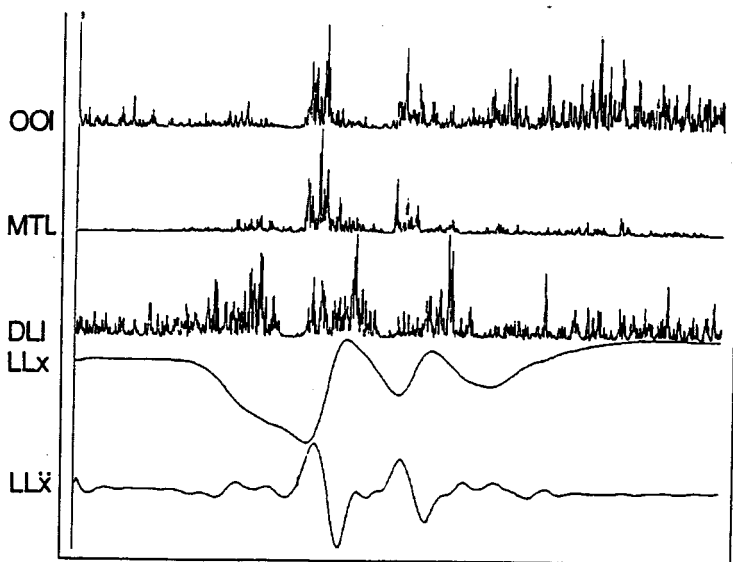


Figure 2b. Rectified muscle activity for an lower lip depressor (depressor labii inferior, DLI), two lower lip elevators (orbicularis oris inferior, OOI, and, mentalis, MTL), lower lip displacement (LLx) and acceleration (bottom trace). For the lower lip, the large positive-going acceleration marks the onset of the segment, followed by phasic bursts of muscle activity in OOI and MTL accompanying the oral closing. This pattern of activation, along with the one presented in 2a, are considered characteristic of all bilabial sounds.

activation patterns which reflect the form of the signal that impinges on lower motor neurons. In part the activation patterns reflect the contribution of the specific articulator to the sound as well as adjustments for the different biomechanical properties of the articulators. The activation patterns for the lip and the jaw muscles, for example, reflect their contribution to closing the oral end of the acoustic tube; the activation patterns are phasic, producing rapid closing movements; and the timing of medial pterygoid action occurs before the labial muscles due to the inertia of the jaw. In contrast, the activation patterns for the pharyngeal constrictors are more tonic and of longer duration reflecting their role in adjusting the tissue impedance of the vocal tract walls. In this regard, these patterns are viewed functionally as representing the essential dynamics of speech movement production and modulated by the differential filtering properties of the biomechanical periphery.

Prior to motor output at the periphery, these characteristic patterns are proposed to have a two or three dimensional spatial representation within, at least, the the primary motor cortex and perhaps other nonprimary motor areas as well. Rather than attempt a hypothetical scheme of the central nervous system

representation, a schematic of a characteristic neuromuscular implementation will be presented. Shown in Figure 3 is a representation of the output signals sent to various neuromuscular components of the vocal tract that produce /p/. Given that many of the details are not currently known, the figure provides only the important neuromuscular components of the pattern. Further, muscle actions are functional grouped such that upper lip depressors (orbicularis oris superior and depressor anguli oris), for example, are only represented based on their articulatory consequences. At this level of observation, the characteristic motor patterns are isomorphic with the gestural constellations in the computationally sophisticated Linguistic Gestural Model (LGM) developed and implemented at Haskins Laboratories by Browman, Goldstein, and colleagues (Browman & Goldstein, 1985, 1986, 1989, 1990) and incorporates the aspects of earlier and more recent properties of the task dynamic model (TD) developed and refined by Saltzman and colleagues (Saltzman, 1986; Saltzman & Kelso, 1987; Saltzman & Munhall, 1989). The major difference (besides the fact that the TD and LGM are computational and this model has no such constraints!) is that much of the details that coordinate task-related vocal tract actions and differentiate sounds of the language are incorporated into stored nervous system elements which effectively reduce the

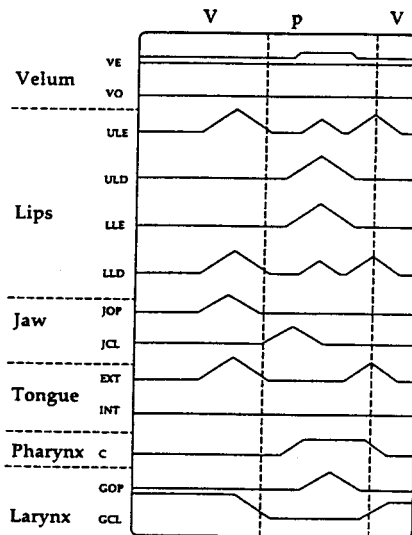


Figure 3. A schematic peripheral representation of a characteristic pattern of vocal tract activation for the bilabial /p/. The dotted lines generally demarcate the segment boundaries. Abbreviations are as follows: VE-velar elevator, VD-velar depressor, ULE-upper lip elevator, ULD-upper lip depressors, LLE-lower lip elevators, LLD-lower lip depressor, JOP-jaw openers, JCL-jaw closers, EXT-extrinsic (tongue muscles), INT-intrinsic, C-constrictors, GOP-glottal opener, GCL-glottal closers.

on-line computational complexity. The rationale for such an approach is that speech as a well-learned (or over learned) motor behavior, incorporates much of its operation into automatic sensorimotor functions.

Within the current model, the characteristic vocal tract configurations and the phonemes of the language are isomorphic. This requires 43 different vocal tract specifications each with its characteristic neuromuscular specifications retained in nervous system memory; 43 is certainly not a number that would tax nervous system storage or processing capabilities. However, it is not clear that this is the fundamental unit of production or that phonemes are an important organizational unit; rather, sound producing vocal tract actions are the lowest level of sensorimotor control. As such, included in Figure 3 are the neuromuscular signals preceding oral closing (associated with a generic vowel) since in most cases opening and closing actions must be tightly coupled. From a sensorimotor perspective, a VC or CVC (opening-closing) organization is more appealing as a unit of speech motor control. As suggested above, inherent in each pattern is the temporal coordination among the constituent components. The time course of activation of the particular components and the particular signal shapes result in consistent and systematic coordinative patterns associated with various sounds. It is not surprising that relative timing is so consistent even in the face of mechanical perturbations (Gracco & Abbs, 1988; Gracco & Löfqvist, 1989; Gracco, 1988). These characteristic patterns can then be modulated according to other task related factors such as the distance to be moved, the overall rate of movement, and the presence of various stress adjustments. The patterns, with their inherent relative timing relations, can be easily compressed or expanded in a systematic manner by modulation of the frequency and/or amplitude of the input signals. It is also likely that the signal shapes vary for different articulators, since each articulator has specific biomechanical properties and such differences have generally been taken into account at least during development. Finally, separate processes extrinsic to the pattern such as those for speech rate and stress specifications should result in a unitary adjustment in all vocal tract structures. The observation of simultaneous respiratory, laryngeal, and oral adjustments accompanying emphatic stress-related manipulations is consistent with this organizational scheme (Fowler, Gracco & V.-Bateson, 1989).

Before proceeding, a number of points should be discussed. First, while vocal tract specifications involve description of individual muscles and sub-muscle actions, it is not being suggested that the child learning to speak has to obtain control over all the individual muscular degrees of freedom. More likely, certain synergies exist, even at birth, that reflect constraints on the sound producing mechanism. As early as the birth cry, the infant is producing coordinated actions of the respiratory, laryngeal and supralaryngeal systems, or a cry would not be possible. As such, patterns are present that can be used as the basis for further differentiation. It is certainly plausible that these fundamental patterns are learned by the child during development based on some fundamental nonspeech actions emerging from breathing, sucking, chewing, swallowing, crying and early

vocalizations. For example, breathing involves opening of the glottis during breathing which must be accompanied by relaxation (or significant reduction) in the activity of laryngeal adductors. Similarly, crying involves coordination of expiration with laryngeal adduction to produce vibration. As the child matures variations of this pattern may form the basis for voicing and devoicing. During chewing a basic pattern of jaw opening, accompanied by relaxation of jaw closing, forms a pattern that can be modified to produce the more variable jaw patterns for speech. Speech motor development may be envisioned as a learning process in which the child makes finer and more varied adjustments in its vocal tract, generalizing from fundamental nonspeech actions, to produced sounds. It is suggested that such actions become fixed once a sound is acquired by the child, and the characteristic neuromuscular pattern becomes a retrievable element in the child's sensorimotor repertoire.

There are a number of reasons for conceptualizing vocal tract actions from a neuromuscular perspective. First, the ability to fractionate control of muscles into functional chunks is consistent with the level of control exercised by the nervous system (English, 1982; Loeb, 1985). This is not to suggest that the nervous system controls muscles as opposed to movements; rather the detailed somatotopy and apparent fractionated control at the level of the motor cortex and brainstem can be exploited during speech acquisition to provide the framework to assemble patterns involving synergistic and part muscle actions. Second, description of the physiological characteristics of speech movements has the potential to provide a level of observation and detail not possible with more traditional kinematic accounts. This perspective captures the essence of the neural signals which co-occur with the contractile forces creating movement. With the concomitant development of realistic biomechanical models or elaboration of the biomechanical properties of the vocal tract, such signals can be used heuristically to determine which aspects of speech movement need to be explained in a control sense and which details emerge from passive biomechanical properties of the articulators. Finally, explicit consideration of the neuromuscular activation of vocal tract components provides insight into the manner in which these characteristic patterns become modified during implementation.

MODIFICATION OF VOCAL TRACT CONFIGURATIONS

To implement any action specific muscles involved can have only one of three distinct states of specification; activated, inhibited, or null. Unspecified articulators (null states) allow contiguous segmental vocal tract actions to intrude resulting in coarticulation (see Fowler, 1980; Kent & Minifie, 1977; Öhman, 1966; Saltzman & Munhall, 1989). Similarly, vocal tract actions involving the same articulator can be blended with the rate of segmental adjustments determining the observable manifestation (see Munhall & Löfqvist, 1990; Stetson, 1951). Vocal tract actions may have contiguous phonetic segments with differing degrees of antagonistic action associated with a particular articulator. In certain contexts,

neighboring submuscle actions of a particular articulator, such as the anterior and posterior portions of the tongue, may result in antagonistic action and articulator undershoot. One of the consequences of explicit consideration of neuromuscular organization is that coarticulation and other related phenomenon involving the smearing of characteristic vocal tract states should be affected by a combination of factors including degree of competition in contiguous segments and the overall speed or frequency of production. Further, if the sensorimotor control scheme outlined in the previous section is correct, there should be certain observations that are concomitant with coarticulatory phenomena. For example, if lip rounding is anticipated from a rounded vowel (/u/ for example) during the production of a nonlabial consonant such as /t/, the tongue body motion and resulting configuration for the /u/ should also show some affect of the intrusion of the /u/ segment. There should be an indication that the entire segment has blended rather than just a feature (see Daniloff & Hammarberg, 1973; Kent & Minifie, 1977 for reviews). In the present scheme, however, the specific coarticulatory influences can not be entirely predicted without a fundamental description and understanding of the neuromuscular configurations associated with specific vocal tract actions. This includes some understanding of the contribution of the biomechanical periphery and the interactions of the anatomical linkages to the sculpting of kinematic patterns (Gracco, 1990). In the following section, the role of peripheral sensory information will be considered as a means to modify the central motor commands.

SENSORY INFLUENCES

An important consideration concerning the sensorimotor control of speech is the influence of various sensory modalities. The specific extent and mode of sensory influences on speech motor output is still a matter of empirical investigation and theoretical contention and is one area that is often overlooked in speech production models. Information extracted from the different sensory modalities forms the basis for communicative, linguistic, or sensorimotor adjustments resulting in global as well as local effects on speech output. There are three sensory channels that have the potential to modify speech motor output each in overlapping but unique ways; visual, auditory, and somatic. During normal speaking situations, visual information regarding ones' vocal tract is not typically available; direct sensorimotor linkages are nonexistent. Rather, visual input is restricted to information regarding the communicative environment and provides what can be thought of as global influences on the motor control process. Faced with an environment that will require sound transmission across relatively long distances such as a classroom or lecture hall, the output intensity that a speaker uses will be adjusted to assure communicative effectiveness. Similarly, speaking to someone who is experiencing auditory acuity difficulties (temporary or permanent) the speaker may also modify the precision of articulatory adjustments to assist the listener. In general, visual information does not appear to play a significant or consistent role in the direct regulation of speech motor output.

Rather, visual-motor influences can be thought of as adaptive and are more likely used for cognitive and certain linguistic adjustments affecting certain global sensorimotor parameters.

To evaluate the potential effects of auditory input on the motor control process, the auditory can be eliminated (temporarily) or distorted in various ways. Some useful information has been obtained using this kinds of experimental approach. For example, long duration exposure to high levels of auditory masking (Kelso & Tuller, 1983; Lane & Tranel, 1971; Ringel & Steer, 1963), delayed auditory feedback (Black, 1951; Fairbanks, 1955; Zimmermann, Brown, Kelso, Hurtig & Forrest, 1988), and low pass filtering (Forrest, Abbas & Zimmermann, 1986) are some of the conditions that can disrupt a subjects' auditory input. However, the issue of whether the modifications observed reflect the lack of auditory information or whether the modifications reflect long term exposure to novel feedback conditions has not been adequately addressed. Since sensory input can have both facilitatory and inhibitory effects on motor output introducing novel conditions for extended periods of time may result in changes that only indirectly, at best, reflect the potential contribution of the sensory modality to the normal motor control process. The best method for auditory disruption to date has been developed by Barlow and Abbs (1978) in which the subjects' own acoustic output (sidetone) is unpredictably eliminated for short durations (200 msec) on a small percentage of experimental trials. While such a paradigm does not provide a natural probe into the system operation, it is much less obtrusive than previous techniques that suffer from potential adaptation effects.

Most researchers would agree that auditory information during speech development is critical to the acquisition of the sound patterns of the language. Long term elimination of auditory information or the lack of auditory information during speech development can severely affect the ability to maintain or acquire speech. As such, auditory input is considered instrumental in developing the characteristic neuromotor patterns that form the basis for the present model. Once acquired, however, the potential role of the auditory system may be limited. Even so, auditory information is still used in a corrective manner as evidenced by the adjustments one makes to slips of the tongue and other kinds of speech errors. In terms of on-line sensorimotor processes, reduced or distorted auditory information has been shown to result in rather subtle deficits in speech output. From some recent experimental evidence some have suggested that auditory information might play a role in the ongoing modulation of speech motor output (Barlow & Abbs, 1978; Forrest, Abbas & Zimmermann, 1986; Zimmermann, Brown, Kelso, Hurtig & Forrest, 1988). The dynamic properties of the acoustic signal can be related in a systematic, albeit nonlinear way, to articulatory motion, and could conceivably be useful in making predictive articulatory adjustments. To date, however, direct experimental evidence is limited.

Early research efforts to assess the potential role of somatic sensory information from skin and muscle receptors located throughout the vocal tract relied on local or nerve block anesthesia to eliminate sensory inflow. Results were

equivocal but suggested to some that somatic sensory information, similar to auditory information, may play a role in speech acquisition but not in the regulation of the speech of adults (see Borden, 1979; Gracco & Abbs, 1987; Perkell, 1980 for reviews). It is doubtful, however, given the extent and degree of sensory innervation in the human vocal tract, that somatic sensory information can ever be truly eliminated. The lack of significant sensory reduction effects noted in some studies, then, suggests that speech can be produced, for a limited time without the full complement of incoming sensory information. This does not necessarily indicate that speech is afferent-independent, but that speech production is an integrated process with distributed and overlapping functions. Eliminating or reducing the contribution of one component of the process results in other components compensating for the loss.

More recently, mechanical loads unexpectedly applied to various articulators have been used to evaluate whether somatic sensory information is important to the ongoing motor control process. The reasoning is that, if sensory receptors located in various regions of the vocal tract are being continuously, or quasi-continuously, monitored during speaking, then disrupting articulatory movement should result in observable compensation. Results have clearly shown that somatic sensory signals have the necessary characteristics to be a useful in the on-line control of speech movements. Somatic sensory adjustments are rapid, usually less than a reaction time, and functionally organized such that the most directly perturbed articulators provide the major adjustment with secondary adjustments seen in anatomically remote functionally-related articulators. The distributed nature of the compensation strongly suggests that sensorimotor interactions, in the form of distributed synaptic linkages, are a feature of the neural organization for speech. Rapid, precise somatotopic and topographic adjustments have, to date, only been demonstrated from analysis of mechanical perturbation suggesting a dominant role for somatic sensory input in the ongoing modulation of speech motor output. This is not to suggest that other sensory modalities do not contribute to the ongoing sensorimotor control process; rather that the experimental evidence is lacking. It appears that the central nervous system is constantly receiving information on all phases of speech production and sensory considerations are as important in understanding motor control as perceptual considerations are important for understanding action.

Perhaps the best way to illustrate the manner in which direct sensory information can be used in the control of movement is to consider the motor task itself. Speaking involves the continuous modulation of the vocal tract producing local and global aerodynamic events structuring the air in characteristic ways. The specific vocal tract configurations are constantly changing during speaking with the same sound exhibiting variable movement patterns dependent on, among other things, phonetic context. From perturbation studies it is known that sensory information from somatic sensory receptors can interact with central motor commands to make short-term (within a few hundred milliseconds) and longer term contextual adjustments in speech motor output. The characteristic neuromuscular

pattern previously presented (Figure 3) can easily be adjusted through the vast sensorimotor linkages within and among vocal tract structures. As such, somatic sensory input from antecedent articulatory events can be used to modulate select properties of the neuromuscular pattern automatically (see Gracco, 1987 for discussion). In the case of a /p/ preceded by either a low vowel a neutral vowel or a high vowel, the oral aperture would reflect different degrees of openness with respect to some neutral or reference level. The somatic sensory input would, based on well established sensorimotor linkages, modulate the neuromotor pattern accordingly. Recent experimental results for bilabial sounds preceded by high or low vowels are consistent with the idea that there is an overall modulation of oral closing actions based on oral opening considerations (see also Folkins & Linville, 1983); an estimation of oral opening can be easily obtained from the jaw movement (or position) associated with the preceding vowel (cf. Gracco, 1987; Gracco, submitted). Further, when the oral opening distance is reduced due to a high vowel preceding closure, the upper and lower lip closing movements are reduced together suggesting that upper and lower lip control signals are modulated together. The resultant modulatory effects of sensorimotor linkages are dependent on a number of factors including the parameters of the central activation signals, and the strength and sign of the synaptic connections (the wiring). Sensorimotor interactions with characteristic neuromotor patterns provide a means to reduce the computational requirements of contextual variations by providing automatic adjustments in the control signals based on the conditions at the periphery.

SEQUENCING OF VOCAL TRACT ACTIONS

Speech is more than the specification of characteristic motor patterns adjusted for context. An important consideration in speech production is the sequencing of vocal tract actions into communicatively meaningful units of production. While speech is a specialized human function, the view taken here is that it is one of many important brain functions and any theoretical account must adhere to principles that are shared by other similar behaviors. If one accepts the premise that the human brain has evolved from earlier brains, (based on the need to predict and control species-specific events in the environment), then supposing that more complex, higher-level behaviors developed from lower level related behaviors, within and across species, is a logical extension. This is not to suggest that speech, locomotion, and handwriting, as examples of sequential motor behaviors, share specific motor patterns; rather, they may share similar mechanisms for their implementation as well as adhere to similar organizational principles (see Grillner, 1982; Kelso & Tuller, 1984). Common organizational principles and sensorimotor processes may be used for speech and other motor behaviors, although they will be adopted to specific task requirements (e.g. communication) and effector properties. Speech and other sequential motor behaviors such as typing, handwriting, locomotion, mastication, and to a lesser

extent respiration involve serial ordering of muscle actions and movements. For more automatic behaviors such as mastication and locomotion, central rhythm generators have been identified which produce behavior-specific rhythmic motor output similar in form and function to those identified in lower vertebrates. Differences in muscle activity and movement patterns for speech, chewing, and respiration clearly indicate that the same central pattern generator does not underlie all behaviors (Moore, Smith & Ringel, 1988; Smith & Denny, 1990).

A number of observations, however, are consistent with the presence of some kind of rhythm generating mechanism or neural network as the basis for sequential speech motor adjustments. For example, compensatory adjustments for lower lip perturbations during an oral closing movement demonstrate changes in interarticulator timing consistent with the operation of an underlying oscillatory or rhythm generating mechanism (Gracco & Abbs, 1988; 1989). Specifically, the timing of the oral closing action is advanced (vowel duration is shortened) if the perturbation occurs prior to the onset of the closing action (Gracco & Abbs, 1988). In a complementary investigation it was also found that if a lip perturbation was unexpectedly removed well in advance of oral closure, the closing action was delayed (vowel duration increased) (Gracco & Abbs, 1989). These results are consistent with a conclusion that phase-related effects of sensory stimuli, resulting from the perturbation, interacting with rhythmic motor output to modify sequential timing. The qualitative observation of spatiotemporal consistency of sequential movements associated with repeated production of sentence-length material (see Gracco, 1990) is also suggestive of an underlying sequencing mechanism. Other results such as minimal movement durational changes to static (Lindblom et al., 1987) and dynamic perturbation (Gracco & Abbs, 1988) are consistent with an underlying mechanism in which sequential timing is maintained.

Recent experiments and theoretical perspectives on the neural control of rhythmic respiratory movements offer an interesting framework for speech movement sequencing (Feldman et al., 1988). It has been suggested that the central pattern generator for respiration may more appropriately be regarded as two separate, but interacting, processes; one specifying the pattern of muscle actions, and one specifying the timing of the output (the rhythm). A similar scheme can be suggested for speech. The characteristic neuromotor patterns for speech sounds outlined above interact with a central rhythm generating process which dictates the timing of the output (see also Saltzman & Munhall, 1989). Two studies of note have attempted to evaluate the apparent rhythmicity of speech. Ohala (1975) recorded over 10,000 jaw movements over a 1.5 hour period of oral reading. Although there were frequencies evident from spectral analysis in the range of 2-6 Hz significant variability was also observed. In contrast, Kelso et al. (1985) reported a rather strong periodicity, with little variability, at approximately 5-6 Hz for lower lip/jaw movements during reiterant speech. The results of the two studies are only contradictory if one assumes that context should not interactively affect rhythmic output. The Ohala study did not constrain the reading material and, hence, reflected a range of phonemic content. Kelso and colleagues, on the other

hand, restricted the phonemic content to "ma" and "ba". It seems more likely, given the intrinsic timing character of various sounds, that output frequency may be modulated by phonemic context; the sounds of the language may have their own intrinsic frequency (timing) properties (cf. Fowler, 1980). For example, vowels can be categorized as long or short, generally related to their average relative duration, and consequently to different speed and extent of jaw opening actions. Similarly, movements of various articulators associated with high pressure consonants are often produced at a faster rate than their voiced low pressure counterparts. As shown recently, the oral closing movement is initiated sooner with a tendency for higher closing movement velocity when the consonant is /p/ as opposed to /b/ or /m/ (Gracco, submitted). It is suggested that a central rhythm generator provides the framework for the sequencing of sound-specific patterns with contain certain intrinsic phoneme-specific differences resulting in the continuous modulation of the basic rhythm.

An important consequence of incorporating a central rhythm generator into a speech production model is the ability to explain rate, stress, and final lengthening

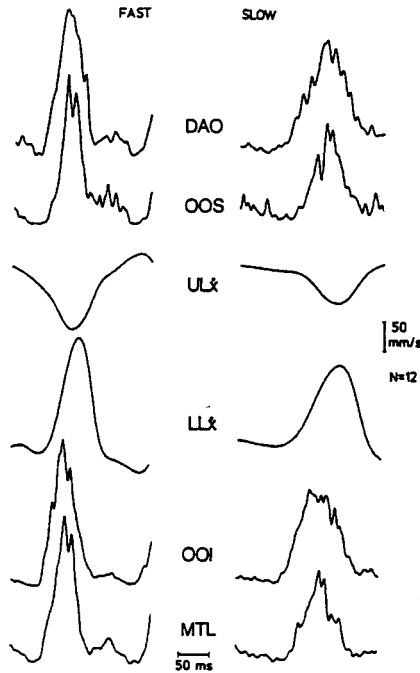


Figure 4. Averaged (n=12) muscle activity for upper lip and lower lip muscles and the associated upper and lower lip closing movement velocities. Subject repeated the word "sapapple" at a fast and slow (subject defined) rate. Averages were aligned to the peak jaw opening velocity (not shown). Although the peak velocities are higher during the fast rate condition, compared to the slow rate condition, the resulting displacements are smaller.

changes with manipulation of a single mechanism; global and local changes in the frequency of the rhythm. Changes in speaking rate can be viewed as an increase in the output of the generator, producing characteristic changes in the segments as well as their sequencing. For example, increasing the output frequency of the generator (increasing speech rate) is accompanied by higher amplitude, shorter duration bursts of muscle activity (see Figure 4 for example, also Gay et al., 1974; Gay & Hirose, 1973) which results in higher movement velocities, as shown in Figure 4, and a reduction in movement displacement (Kelso et al., 1985). The reduction in movement displacement is a consequence of greater gestural overlap (Browman & Goldstein, 1989; Saltzman & Munhall, 1989) effectively increasing the damping. Similarly, stress and final lengthening can be viewed as a local decrease in the output frequency. It is the case that phrase-final lengthening and stress manifest different kinematic effects (see Edwards, Beckman & Fletcher, 1991). However, these may merely reflect differences in context such that phrase final articulations are less constrained because of the relative time between it and the next segment, and the movement continues longer and farther as a consequence; there is no active mechanism to arrest the movement. The possibility that a central rhythm generator underlies the serial timing is an attractive hypothesis that is in need of empirical validation.

POTENTIAL NEURAL MECHANISMS

From the previous discussion, it has been suggested that there are multiple functional processes underlying the generation and sequencing of speech movements. These processes include phonological (vocal tract) specification, sensorimotor integration, and sequencing of sound-producing elements. A fundamental premise in the present model is that there are characteristic patterns stored in the nervous system whose selection and activation initiate events which ultimately produce coordinated sequential vocal tract actions. At present any attempt to speculate on where or how such patterns are stored would be premature. However, it is possible to consider the sensorimotor implementation of these hypothetical patterns as well as to generally speculate on the contribution of various distributed neuroanatomical systems that are known to be involved in speech production (cf. Abbs, 1986; Gracco & Abbs, 1987; Kent, 1990 for reviews).

In humans, acquired lesions posterior to the central sulcus result in a form of fluent aphasia characterized by varying degrees of phonological impairment (Blumstein et al., 1977; Blumstein et al., 1980; Tuller, 1984). Given the large representation of facial structures, and the projections to supplementary and premotor cortices (Wiesendanger & Weiesendanger, 1984; Petrides & Pandya, 1984), posterior parietal cortex (area 7b), having sensory, motor, and behavioral functions (Hyvärinen, 1981; 1982), seems a likely candidate for the instantiation of phonological goals. As suggested above, it is not clear where the phonological specifications are stored, but once recalled from memory the posterior parietal region may be involved in the setting up of a number of neuroanatomical system

used for the implementation of speech motor actions. As such, posterior parietal and no doubt portions of frontal cortex, are "upstream" from the sensorimotor implementation of speech production and can be viewed as performing a prescriptive or executive function.

In contrast, two major brain systems, involving the basal ganglia and supplementary motor area (SMA) and the cerebellum and pre-motor area (PM), are viewed as the major implementation centers to carry out the details of the speech production process. The function of the basal ganglia-SMA system, surmised from human lesion and behaving nonhuman primate studies, appears to have the requisite function to be involved in scaling the hypothesized characteristic neuromotor patterns in the present model. For example, behavioral data from the human limb studies (see Marsden, 1984 for review) and focal stimulation and lesion data from behaving nonhuman primates in which the primary deficit was an inability to scale muscle actions (DeLong, Alexander, Georgopoulos, Crutcher, Mitchell & Richardson, 1984; Horak & Anderson, 1984a&b). SMA lesions appear to exaggerate the inability to scale muscle actions to task, often resulting in total speech arrest (Arseni & Botez, 1961; Caplan & Zervas, 1978) and a pronounced reduction in self-initiated voluntary movement (see Wiesendanger, 1985 for review). Parkinson's disease results in speech movement impairments that reflect generalized reduction in the speed, and extent of articulatory movements resulting in perceptually distorted consonants, slowed speech rate, and a tendency toward monotone. It is suggested that these deficits reflect a generalized reduction in the ability to scale muscle actions to the specific speech movement requirements. Consistent with the location of the basal ganglia upstream from motor cortex and the relatively indirect access of direct sensory information, it is suggested that the neuromuscular scaling operation is controlled by cortical influence, predominantly the SMA with secondary influences from other cortical areas (Alexander, DeLong, & Strick, 1986).

Speech movement deficits associated with Parkinson's disease do not demonstrate impairments in the duration of the individual movements (Connor et al, 1989; Forrest et al., 1989) suggesting that the basal ganglia is not involved in the sequencing of movements. However, aphasic patients with anterior cortical lesions and ataxic dysarthrics demonstrate a sequencing difficulty manifest in voice onset timing (see Baum et al., 1990; Blumstein et al., 1977; 1980), a sequencing difficulty consistent with damage to the premotor area which receives projections from the cerebellum, a neural structure involved in timing movement sequences (Kent & Rosenbeck, 1982; Gracco & Abbs, 1987; Ito, 1984). Similarly, neurophysiological investigations in nonhuman primates have shown the PMA to be involved in the sensory guidance of movements (Godschalk, Lemon, Nijs & Kuypers, 1981; Halsband & Passingham, 1982; Rizzolatti, Scandolaara, Matelli & Gentilucci, 1981) similar to the function proposed for the cerebellum (Ito, 1984; Soechting, Ranish, Palminteri & Terzuolo, 1976). In general, the cerebellar-PM system appears to function as an important component in the incorporation of peripheral sensory signals into the central motor commands.

The final component in the present model is the hypothesized central rhythm generator. While there is no evidence that the cerebellum is the site of a central rhythm generator for any motor action, it has been suggested by Ito (1984) that the cerebellum may contribute to the timing of many rhythmic motor behaviors. The speech timing changes associated with cerebellar damage is consistent with at least a contributing role. Other considerations for the locus of a central rhythm generator would be the intricate synaptic connections within the brainstem that could possibly be temporarily set into oscillation by directed input from cortical structures, similar to the central masticatory rhythm generator (Nakamura, 1986 for example). An alternate possibility is that speech rhythm and hence serial timing is a network property that emerge from a hierarchical organization (Martin, 1972). It is clear that a definitive answer to the presence and possible location of a central rhythm generator underlying speech timing will require a great deal more experimental consideration.

One prediction from the sensorimotor organization presented in the present chapter in which the vocal tract is considered the smallest functional control structure operated on by sensorimotor scaling and timing processes is the absence of subphonemic speech errors as would occur with speech subsystem impairment (Abbs, Hunker, & Barlow, 1983). Except for cases of focal nervous system damage such as a dystonia, or lower motoneuron damage, speech motor impairments specific to an articulatory subsystem should not occur. The deficits associated with various nervous system damage may result in different degrees of impairment because of the biomechanical or physiological differences of individual articulators. However, it is not clear that surface differences are a true reflection of underlying differential deficits. For a variety of speech motor disorders due to damage to basal ganglia, cerebellum and anterior and posterior cortical areas, deficits are observed that are consistent with a global rather than focal breakdown. That is, the major neuroanatomic sensorimotor systems involved in speech production including the basal ganglia-supplementary motor system, cerebellar-premotor cortical system, and inferior parietal cortex, appear to function, not in the control of movement per se, but in processes from which movement emerges.

SUMMARY

The framework that emerges from the preceding is that speech motor control involves a small number of sensorimotor processes applied in a unitary manner to the vocal tract and modulated according to task requirements such as speech rate, articulatory precision, and suprasegmental stress. In the current model, these processes include selection and activation of characteristic vocal tract actions, spatiotemporally scaled according to phonological considerations, such as intrinsic timing properties, and peripheral conditions. Somatic sensory information is an important component of the system allowing dynamic modulation of relatively stereotypic motor commands. An underlying rhythmic mechanism is proposed

which provides the temporal framework for sequential speech adjustments as well as a mechanism to systematically vary suprasegmental speech timing. These fundamental sensorimotor processes interact and overlap to produce the continuous dynamic modulation of the vocal tract generating time-varying pressures and flows. An important constraint on the model is that the underlying processes are consistent with generally accepted nervous system operations. An important prediction from the model is that nervous system damage, unless extremely focal, should produce global deficits attributable to one or some combination of three major nervous system functions for speech; pattern specification, scaling of muscle actions, and initiation and sequencing of the production units.

ACKNOWLEDGEMENTS

The writing of this paper was supported by NIH grants DC-00121 and DC-00594. Carol Fowler is acknowledged for helpful comments.

REFERENCES

- Abbs, J.H. & Gracco, V.L. (1984). Control of complex motor gestures: Orofacial muscles responses to load perturbation of the lip during speech. *Journal of Neurophysiology*, 51, 705-723.
- Abbs, J.H., Gracco, V.L. & Cole, K.J. (1984). Control of multimovement coordination: Sensorimotor mechanisms in speech motor programming. *Journal of Motor Behavior*, 16, 195-232.
- Abbs, J.H., Hunker, C. & Barlow, S. (1983). Differential speech motor subsystem impairments with suprabulbar lesions: Neurophysiological framework and supporting data. In: W. Berry (Ed.), *Clinical Dysarthria* (pp. 21-56). San Diego: College Hill Press.
- Atkeson, C.G. & Hollerbach, J.M. (1985). Kinematic features of unrestrained vertical arm movements. *Journal of Neurosciences*, 5, 2318-2330.
- Alexander, G.E., DeLong, M.R. & Strick, P.L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annals of Review Neuroscience*, 9, 357-381.
- Barlow, S.M. & Abbs, J.H. (1978). Some evidence of auditory feedback contributions to ongoing speech motor control. Paper presented at the American Speech and Hearing Convention, San Francisco, CA.
- Baum, S., Blumstein, S., Naeser, M. & Palumbo, C. (1990). Temporal dimensions of consonant and vowel production: an acoustic and CT scan analysis of aphasic speech. *Brain and Language*, 39, 33-56.
- Black, J.W. (1951). The effect of delayed sidetone upon vocal rate and intensity. *Journal of Speech and Hearing Disorders*, 16, 56-60.
- Blumstein, S., Cooper, W., Goodglass, H., Statlender, S. & Gottlieb, J. (1980). Production deficits in aphasia: a voice-onset time analysis. *Brain and Language*, 9, 153-170.
- Blumstein, S., Cooper, W., Zurif, E. & Caramazza, A. (1977). The perception and production of voice-onset time in aphasia. *Neuropsychologia*, 15, 371-383.
- Borden, G.J. (1979). An interpretation of research on feedback interruption in speech. *Brain and Language*, 7, 309-319.
- Browman, C.P. & Goldstein, L. (1985). Dynamic modeling of phonetic structure. In: V. Fromkin (Ed.), *Phonetic linguistics* (pp. 35-53). New York: Academic Press.
- Browman, C.P. & Goldstein, L. (1986). Towards an articulatory phonology. *Phonology Yearbook*, 3, 219-252.
- Browman, C.P. & Goldstein, L. (1989). Articulatory gestures as phonological units. *Phonology*, 6, 250-251.

- Browman, C.P. & Goldstein, L. (1990). Gestural specification using dynamically-defined articulatory structures. *Journal of Phonetics*, 18, 299-320.
- Chen, M. (1970). Vowel length variation as a function of the voicing of the consonant environment. *Phonetica*, 22, 129-159.
- Cohen, A.H., Rossignol, S. & Grillner, S. (1988). *Neural control of rhythmic movements in vertebrates*. New York: Wiley.
- Connor, N.P., Abbs, J., Cole, K.J. & Gracco, V.L. (1989). Parkinsonian deficits in serial multiarticulate movements for speech. *Brain*, 112, 997-1009.
- Churchland, P.S. (1986). *Neurophilosophy: Toward a unified science of the mind/brain*. Cambridge, Mass: MIT Press.
- Churchland, P.M. (1989). *A neurocomputational perspective: The nature of mind and the structure of science*. Cambridge, Mass: MIT Press.
- Daniiloff, R.G. & Hammarberg, R.E. (1973). On defining coarticulation. *Journal of Phonetics*, 1, 239-248.
- DeLong, M.R., Alexander, G.E., Georgopoulos, A.P., Crutcher, M.D., Mitchell, S.J. & Richardson, R.T. (1984). Role of basal ganglia in limb movements. *Human Neurobiology*, 2, 235-244.
- Edelman, S. & Flash, T. (1987). A model of handwriting. *Biological Cybernetics*, 57, 25-36.
- Edwards, J., Beckman, M.E. & Fletcher, J. (1991). The articulatory kinematics of final lengthening. *Journal of the Acoustical Society of America*, 89, 369-382.
- English, A.W. (1982). Are whole muscles the fundamental substrate for the CNS control of movement? *Behavioral Brain Sciences*, 5, 544-545.
- Fairbanks, G. (1955). Selective vocal effects of delayed auditory feedback. *Journal of Speech and Hearing Disorders*, 20, 333-346.
- Feldman, J.L., Smith, J.C., McCrimmon, D.R., Ellenberger, H.H. & Speck, D.F. (1988). Generation of respiratory patterns in mammals. In: A.H. Cohen, S. Rossignol and S. Grillner (Eds.), *Neural control of rhythmic movements in vertebrates* (pp. 73-100). New York: Wiley and Sons.
- Folkins, J.W. & Abbs, J.H. (1975). Lip and jaw motor control during speech: Responses to resistive loading of the jaw. *Journal of Speech and Hearing Research*, 18, 207-220.
- Folkins, J.W. & Linville, R.N. (1983). The effects of varying lower-lip displacement on upper-lip movements: Implications for the coordination of speech movements. *Journal of Speech and Hearing Research*, 26, 209-217.
- Forrest, K., Abbas, P. & Zimmermann, G.N. (1986). Effects of white noise masking and low pass filtering on speech kinematics. *Journal of Speech and Hearing Research*, 29, 549-562.
- Forrest, K., Weismer, G. & Turner, G. (1989). Kinematic, acoustic, and perceptual analyses of connected speech produced by Parkinsonian and geriatric adults. *Journal of the Acoustical Society of America*, 85, 2608-2622.
- Fowler, C.A. (1980). Coarticulation and theories of extrinsic timing. *Journal of Phonetics*, 8, 113-133.
- Fowler, C.A. (1983). Converging sources of evidence on spoken and perceived rhythms of speech: Cyclic production of vowels in monosyllabic stress feet. *Journal of Experimental Psychology*, 112, 86-112.
- Fowler, C.A., Rubin, P., Remez R.E. & Turvey, M.T. (1980). Implications for speech production of a general theory of action. In: B. Butterworth (Ed.), *Language Production* (pp. 373-420). New York: Academic Press.
- Fowler, C.A. & Turvey, M.T. (1980). Immediate compensation in bite-block speech. *Journal of Phonetics*, 37, 306-326.
- Fowler, C.A., Gracco, V.L. & V.-Bateson, E. (1989). Remote and local effects of stress within and among articulatory subsystems. *Journal of the Acoustical Society of America*, 86(1), S115.
- Flashner, H., Beuter, A. & Arabyan, A. (1988). Fitting mathematical functions to joint kinematics during stepping: Implications for motor control. *Biological Cybernetics*, 58, 91-99.
- Gay, T. & Hirose, H. (1973). Effect of speaking rate on labial consonant production. *Phonetica*, 27, 44-56.

- Gay, T., Ushijima, T., Hirose, H. & Cooper, F.S. (1974). Effect of speaking rate on labial consonant-vowel articulation. *Journal of Phonetics*, 2, 47-63.
- Getting, P.A. (1989). Emerging principles governing the operation of neural networks. *Annual Review of Neuroscience*, 12, 185-204.
- Godschalk, M., Lemon, R., Nijs, H. & Kuypers, H. (1981). Behavior of neurons in monkey peri-arcuate and precentral cortex before and during visually guided arm and hand movements. *Experimental Brain Research*, 44, 113-116.
- Gracco, V.L. (1987). A multilevel control model for speech motor activity. In: H. Peters and W. Huistijn (Eds.), *Speech motor dynamics in stuttering* (pp. 57-76). Wien: Springer-Verlag.
- Gracco, V.L. (1988). Timing factors in the coordination of speech movements. *Journal of Neuroscience*, 8, 4628-4634.
- Gracco, V.L. (1990). Characteristics of speech as a motor control system. In: G.R. Hammond, (Ed.), *Cerebral control of speech and limb movements* (pp. 3-28). North-Holland: Elsevier.
- Gracco, V.L. Some organizational principles for speech movement control. (submitted) *Journal of the Acoustical Society of America*.
- Gracco, V.L. & Abbs, J.H. (1985). Dynamic control of the perioral system during speech: kinematic analyses of autogenic and nonautogenic sensorimotor processes. *Journal of Neurophysiology*, 54, 418-432.
- Gracco, V.L. & Abbs, J.H. (1986). Variant and invariant characteristics of speech movements. *Experimental Brain Research*, 65, 156-166.
- Gracco, V.L. & Abbs, J.H. (1988). Central patterning of speech movements. *Experimental Brain Research*, 71, 515-526.
- Gracco, V.L. & Abbs, J.H. (1989). Sensorimotor characteristics of speech motor sequences. *Experimental Brain Research*, 75, 586-598.
- Gracco, V.L. & Löfqvist (1989). Speech movement coordination: Oral-laryngeal interactions. *Journal of the Acoustical Society of America*, 86, S114.
- Halsband, U. & Passingham, R. (1982). The role of premotor and parietal cortex in the direction of action. *Brain Research*, 240, 368-372.
- Harris, K.S. (1978). Vowel duration and its underlying physiologic mechanisms. *Language and Speech*, 21, 354-361.
- Henke, W.L. (1966). *Dynamic articulatory model of speech production using computer simulation*. Unpublished doctoral dissertation, Massachusetts Institute of Technology.
- Hollerbach, J.M. (1981). An oscillation theory of handwriting. *Biological Cybernetics*, 39, 139-156.
- Horak, F.B. & Anderson, M.E. (1984a). Influence of globus pallidus on arm movements in monkeys. I. Effects of kainic acid-induced lesions. *Journal of Neurophysiology*, 52, 290-304.
- Horak, F.B. & Anderson, M.E. (1984b). Influence of globus pallidus on arm movements in monkeys. II. Effects of stimulation. *Journal of Neurophysiology*, 52, 305-322.
- Hyvärinen, J. (1981). Regional distribution of functions in parietal association area 7 of monkey. *Brain Research*, 206, 287-303.
- Hyvärinen, J. (1982). *The parietal cortex of monkey and man*. Berlin: Springer-Verlag.
- Ito, M. (1984). *The cerebellum and neural control*. New York: Raven Press.
- Jackson, J. Hughlings (1875). Clinical and physiological researches on the nervous system. (Contains a reprinting of "On the anatomical and physiological localisation of movement in the brain," first published in *Lancet* 1873, i:84-85.) Churchill: London.
- Joos, M. (1948). Acoustic phonetics. *Language*, 24, 1-136.
- Kelso, J.A.S. & Tuller, B. (1983). "Compensatory articulation" under conditions of reduced afferent information: A dynamic formulation. *Journal of Speech and Hearing Research*, 26, 217-224.
- Kelso, J.A.S. & Tuller, B. (1984). Converging evidence in support of common dynamic principles for speech and movement coordination. *American Journal of Physiology*, 15, R928-R935.
- Kelso, J.A.S., Tuller, B.V.-Bateson, E. & Fowler, C. (1984). Functionally specific articulatory cooperation following jaw perturbations during speech: Evidence for coordinative structures. *Journal of Experimental Psychology*, 10, 812-832.

- Kelso, J.A.S. (1986). Pattern formation in speech and limb movements involving many degrees of freedom. In: H. Heuer and C. Fromm (Eds.), *Generation and Modulation of Action Patterns* (pp. 105-128). Berlin: Springer-Verlag.
- Kent, R.D. (1990). The acoustic and physiological characteristics of neurologically impaired speech movements. In: W. Hardcastle and A. Marchal (Eds.), *Speech Production and Modelling* (pp. 365-401). Dordrecht: Kluwer Academic Publishers.
- Kent, R.D. & Minifie F.D. (1977). Coarticulation in recent speech production models. *Journal of Phonetics*, 5, 155-133.
- Kent, R.D. & Rosenbek, J.C. (1982). Prosodic disturbances and neurologic lesion. *Brain and Language*, 15, 259-291.
- Kugler, P.N., Kelso, J.A.S. & Turvey, M.T. (1980). On the concept of coordinative structures as dissipative structures: I. Theoretical lines of convergence. In: G.E. Stelmach (Ed.), *Tutorials in motor behavior* (pp. 3-47). Amsterdam: Elsevier/North Holland.
- Lacquaniti, F. (1989). Central representations of human limb movement as revealed by studies of drawing and handwriting. *Trends in Neuroscience*, 12, 287-291.
- Lane, H.L. & Tranel, B. (1971). The Lombard sign and the role of hearing in speech. *Journal of Speech and Hearing Research*, 14, 677-709.
- Lindblom, B., Lubker, J., Gay, T., Lyberg, P., Brander, P. & Holgren, K. (1987). The concept of target and speech timing. In: R. Channon and L. Shockey (Eds.), *In Honor of Ilse Lehiste* (pp. 161-181). Dordrecht, The Netherlands: Foris Publications.
- Loeb, G.E. (1985). Motoneuron task groups: Coping with kinematic heterogeneity. *Journal of Experimental Biology*, 115, 137-146.
- Löfqvist, A. (1990). Speech as audible gestures. In: W. Hardcastle and A. Marchal (Eds.), *Speech production and modelling* (pp. 289-322). Dordrecht: Kluwer Academic Publishers. 289-322.
- Löfqvist, A. & Yoshioka, H. (1981). Interarticulator programming in obstruent production. *Phonetica*, 38, 21-34.
- Löfqvist, A. & Yoshioka, H. (1984). Intra-segmental timing: Laryngeal-oral coordination in voiceless consonant production. *Speech Communication*, 3, 279-289.
- Marsden, C.D. (1984). Which motor disorder in Parkinson's disease indicates the true motor function of the basal ganglia? In: D. Evered and M. O'Connor (Eds.), *Functions of the basal ganglia* (pp. 225-236). London: Pitman.
- Martin, J.G. (1972). Rhythmic (hierarchical) versus serial structure in speech and other behavior. *Psychological Review*, 79, 487-509.
- McClelland, J.L. & Rumelhart, D.E. (1986). *Parallel distributed processing: Explorations in the microstructure of cognition. Vol 2: Applications*. Cambridge, Mass: MIT Press.
- Marr, D. (1982) *Vision*. San Francisco: W.H. Freeman.
- Moore, C.A., Smith, A. & Ringel, R.L. (1988). Task-specific organization of activity in human jaw muscles. *Journal of Speech and Hearing Research*, 31, 670-680.
- Morasso, P. (1981). Spatial control of arm movements. *Experimental Brain Research*, 42, 223-227.
- Morasso, P. & Mussa-Ivaldi, F.A. (1982). Trajectory formation and handwriting: a computational model. *Biological Cybernetics*, 45, 131-142.
- Nakamura, Y. (1986). Neural basis of rhythm generation of masticatory jaw movements. *Progress on Neural Research*, 30, 237-250.
- Ohala, J.J. (1975). The temporal regulation of speech. In: G. Fant and M.A.A. Tatham, (Eds.), *Auditory analysis and perception of speech* (pp. 431-454). London: Academic.
- Öhman, S.E.G. (1966). Coarticulation in VCV utterances: spectrographic measurements. *Journal of the Acoustical Society of America*, 39, 151-168.
- Pellionisz, A. & Llinas, R. (1979). Brain modeling by tensor network theory and computer simulation. The cerebellum: Distributed processor for predictive coordination. *Neuroscience*, 4, 323-348.
- Pellionisz, A. & Llinas, R. (1985). Tensor network theory of the metaorganization of functional geometries in the central nervous system. *Neuroscience*, 16, 245-273.

- Perkell, J.S. (1980). Phonetic features and the physiology of speech production. In: B. Butterworth, (Ed.), *Language Production* (pp. 337-372). New York: Academic Press.
- Petrides, M. & Pandya, D.N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *Journal of Comparative Neurology*, 228, 105-116.
- Rizzolatti, G., Scandolaro, C., Matelli, M. & Gentilucci, M. (1981). Afferent properties of periarculate neurons in macaque monkeys. I. Somatosensory responses. *Behavioral Brain Research*, 2, 125-146.
- Saltzman, E.L. (1986). Task dynamic coordination of the speech articulators: a preliminary model. In: H. Heuer and C. Fromm (Eds.), *Generation and modulation of action patterns* (pp. 129-144), Berlin: Springer-Verlag.
- Saltzman, E.L. & Kelso, J.A.S. (1987). Skilled actions: A task dynamic approach. *Psychological Review*, 94, 84-106.
- Saltzman, E.L. & Munhall, K. (1989). A dynamical approach to gestural patterning in speech production. *Ecological Psychology*, 1, 333-382.
- Shaiman, S. (1989). Kinematic and electromyographic responses to perturbation of the jaw. *Journal of the Acoustical Society of America*, 86, 78-87.
- Smith, A. & Denny, M. (1990). High frequency oscillations as indicators of neural control mechanisms in human respiration, mastication and speech. *Journal of Neurophysiology*, 63, 745-758.
- Soechting, J.F., Ranish, N.A., Palminteri, R. & Terzuolo, C.A. (1976). Changes in a motor pattern following cerebellar and olivary lesions in the squirrel monkey. *Brain Research*, 105, 21-44.
- Stetson, R.H. (1951). *Motor phonetics: A study of speech movements in action*. North Holland: Amsterdam.
- Tuller, B. (1984). On categorizing aphasic speech errors. *Neuropsychologia*, 22, 547-557.
- Tuller, B. & Kelso, J.A.S. (1984). The timing of articulatory gestures: Evidence for relational invariants. *Journal of the Acoustical Society of America*, 76, 1030-1036.
- Tuller, B., Kelso, J.A.S. & Harris, K.S. (1982). Interarticulator phasing as an index of temporal regularity in speech. *Journal of Experimental Psychology*, 8, 460-472.
- Turvey, M.T. (1977). Preliminaries to a theory of action with reference to vision. In: R. Shaw and J. Bransford (Eds.), *Perceiving, acting and knowing: Toward an ecological psychology* (pp. 211-265). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Wiesendanger, M. & Wiesendanger, R. (1984). The supplementary motor area in light of recent investigations. *Experimental Brain Research*, 9, 382-392.
- Zimmermann, G.N., Brown, C., Kelso, J.A.S., Hurtig, R. & Forrest, K. (1988). The association between acoustic and articulatory events in a delayed auditory feedback paradigm. *Journal of Phonetics*, 16, 437-451.