

Chapter 3

1113

A NEUROMOTOR PERSPECTIVE ON SPEECH PRODUCTION

Vincent L. Gracco

Speech is one of man's most distinguishing traits. At the core of this important communicative behavior is the human nervous system which constantly receives, integrates, and exchanges information on the various operations carried out through a variety of sensorimotor channels. In order to understand speech communication it is essential to understand the machine itself, not only at the level of the physical apparatus but at the level of the physiological components and associated processes. An important assumption is that control principles that govern speech and language production and perception are best understood and unambiguously inferred from a perspective that is grounded in nervous system physiology. The focus of this chapter is to outline a theoretical framework for speech production which explicitly takes into account the contribution of the anatomy and physiology of the speech production mechanism as well as information on general nervous system functions and associated regions known to be involved in speech and language production.

INTRODUCTION

The act of speaking and the processes associated with communication are potentially valuable sources of information on the organization and development of human behavior. Empirical observations are critical for developing an understanding of the fundamental components of communicative behavior, how they develop and how they break down. Empirical observations also can be used to infer nervous system functions associated with this complex and intricate process. Attempts to understand, predict and ultimately formulate a systematic body of scientific knowledge about fundamental aspects of speech and language behavior require two additional elements: models and theories. Since these terms are often inconsistently defined in textbooks they will be defined for the sake of clarity. A model is a set of symbols and associated logical rules for manipulating the symbols. The symbols may be numbers, words, physical objects, or abstract forms. The rules may be explicit or implicit. When the symbols of a model are identified with specific empirical events, the model and set of identifications constitute a theory. A theory specifies the relationship between events for the purpose of explanation or prediction. The level of model description determines, to a large extent, the types of explanations one develops. While often overlooked, models and theories are statements of a philosophical perspective on science and the nature of explanation.

In attempting to understand speech and language one of two philosophical perspectives can be taken. These perspectives have historical roots in natural philosophy. The first approach has its roots in early epistemology and is represented by the philosophical position of Plato, described as substance dualism. Plato's theory postulated two different kinds of substances, one from the mind and one from the material world. For the substance dualist, models of behavior would not need to be constrained by considerations of the form or function of the nervous system, since it is impossible to know about them in an empirical or epistemological sense. As described by Churchland (1986), "Plato is the archetypal antinaturalist and contrasts vividly with contemporary naturalists who argue that the mind is the brain and that empirical science is indispensable to discovering the nature of the mind-brain...". Naturalism, on the other hand, suggests that scientific laws are adequate to account for all phenomena. One important implicit difference between substance dualism and naturalism is a lack of distinction between the mind and brain and the consequence that empirical investigation can be used to learn about the psychological events that are not directly observable. It is the latter perspective that provides the philosophical foundation for much of the current work in contemporary neuroscience and leads quite naturally to "... the possibility of a unified theory of the mind-brain, wherein psychological states and processes are explained in terms of neuronal states and processes." (Churchland, 1986).

An approach in which model constructs and theoretical constraints are grounded in neurobiology represents a reductionistic perspective. Reductionism, as pointed out by Churchland (1986), is a widely misunderstood philosophical position. Reductionism is often identified with an attempt to simply some complex behavior to the point where empirical investigation become tractable. However, in the philosophy of science..., "... reduction is first and foremost a relation between theories" in which "...one theory, the *reduced* theory T_r , stands in a certain relation to another more basic theory T_b ." Moreover, "Statements that a phenomenon P_r reduces to another phenomenon P_b are derivative upon the more basic claim that the theory that characterizes the first reduces to the theory that characterizes the second." An example provided by Churchland relates to the theory of optics in which, during the mid-nineteenth century, it was supposed that light and electromagnetic effects were two different kinds of phenomena. By the turn of the century the theory of optics had been reduced to the theory of electromagnetic radiation such that light was now identified as electromagnetic radiation. As more and more information is acquired, due to advances in technology and concomitant changes in experimental design, the expression of psychological theories and model constructs within a neurobiological framework will proceed. From this general philosophical perspective it logically follows that a speech production model should ultimately be reducible to a theory describing how neuronal ensembles work and it should reduce in such a way that the components of the model can be identified with neuronal components. The ultimate reducibility of psychological (or other hypothetical) constructs of speech and language to neuronal processes will only be achieved with considerable time and effort. A necessary first step is the generation of speech production theories and models with a focus on physiological descriptions and behavioral explanations in terms of general nervous

system principles and processes.

CONCEPTUAL FRAMEWORK

A current view in the psycholinguistic literature is that two broad processes underlie language formulation (Levelt, 1989; 1992; Garrett, 1991). The first process involves grammatical encoding, or the creation of lexical items within a syntactic frame, and phonological encoding, including the specification of prosodic structure. These two broad processes create the phonetic plan. The phonetic plan interfaces with speech motor processes that generate the sequence of sounds specified in the plan. The phonological structure of the language interfaces seamlessly with the speech motor processes. The framework presented here incorporates a sensorimotor model of speech production with units of production and mechanisms for activating, scaling and sequencing the units for fluent speech. Aspects of the process have been detailed in various forms in a number of related publications (cf. Abbs, Gracco, & Cole, 1984; Gracco, 1987; 1988; 1990; 1991; 1994; Gracco & Abbs, 1987; 1989; Gracco & Löfqvist, 1994). What is of interest is the identification of the fundamental processes or components of the behavior and whether and how they are represented by known nervous system functions. As is often the case, observation of any behavior at one level of organization may yield patterns that emerge from the influence of or organization at another level of observation. Without considering the multiple levels of organization that exist for any behavior, one can easily generate an over-specified model and an unnecessarily detailed theory. One such level in speech production is the patterns and variations in kinematic observables. As a starting point, the structural and biomechanical properties of the vocal tract will be examined as possible contributors to the complex kinematic patterns observed during speech production, followed by some specific examples of how a neuromotor perspective can lead to simple explanations for apparently complex speech production phenomena.

STRUCTURAL PROPERTIES

The human vocal tract displays a number of biophysical properties that may influence speech kinematics. Whereas the tongue and lips are soft tissue structures that undergo substantial viscoelastic deformation during speech, the jaw displays a degree of anisotropic tension (Lynn & Yemm, 1971). Even seemingly homogeneous structures like the upper and lower lips display different stiffness properties (Ho et al., 1982) which may contribute to their differential movement patterns (Gracco & Abbs, 1986; Gracco, 1988). The mandible is a rigid body exhibiting rotational and translational motion while the tongue is a deformable, volume-preserving solid with a complex tissue structure and muscular organization. In addition to the structural arrangement of the vocal tract muscles for valving and shaping actions, mechanical properties of individual vocal tract structures provide insight into the functional organization of the speech motor control system. The dynamic nature of the tissue load against which the different vocal tract muscles contract is extremely heterogeneous. For

some structures such as the lips and vocal folds, inertial considerations are minimal, while for the jaw and respiratory structures inertia is a significant consideration.

Considering the structural arrangement of the vocal tract, the different muscular orientations and the vast interconnection of muscles, cartilages, and ligaments, it is clear that complex biomechanical interactions are the rule. Passive or reactive changes due to inherent mechanical coupling is a consequence of almost any vocal tract action, with the relative significance varying according to the specific structural components and conformational change and the speed at which adjustments occur. As a result, a single articulatory action may generate primary as well as secondary effects throughout the vocal tract. It is important to determine the contribution of individual articulatory actions to the sound producing process. However, individual articulatory actions never have isolated effects. The combination of the viscoelastic properties of the tissues, the different biomechanical properties of vocal tract structures, and the complex geometry of the vocal tract comprises a complex biomechanical environment. The kinematic and acoustic variability characteristic of speech production reflects in part the differential filtering of neural control signals by the peripheral biomechanics. Recently, a physiological model of human mandible and hyoid motion (Laboissière et al., 1996) was used to show that certain patterns of intra-articulator coarticulation could be explained, not by active movement planning, but by the dynamics of the system at the level of the biomechanics (Ostry et al., 1996). The clearest example, and the one most relevant to separating active versus passive phenomena, was related to movement variations associated with anticipatory coarticulation. An often reported result is that the maximum articulator position of the C in a VCV sequence varies systematically with the height of the the final V. This variation has been explained as reflecting either an explicit planned response of the speech production system or the result of temporal overlap of central commands. However, simulations of the jaw motion using a physiological model clearly demonstrated that the anticipatory variations in the empirical data were the result of muscle mechanics and jaw dynamics, not central control.

In a study in progress, we have found that in certain other contexts systematic changes in observed jaw kinematics cannot be explained by biomechanical considerations (Gracco et al., in preparation). Empirical observations of the initial jaw position (prior to movement) for the initial C in a CVC sequence revealed that jaw position was being varied in anticipation of the upcoming vowel-related movement.

Shown in Figure 1 is the average pitch of the jaw for six subjects obtained during a steady state associated with the consonants /s/, /t/, /f/, and /k/ when followed by the vowel /a/, /i/, or /o/. As can be seen, the pitch of the jaw is lowest for the vowel /a/, slightly higher for the vowel /o/ and highest for the high vowel /i/. This pattern is consistent for all six subjects suggesting that jaw position for a syllable initial consonant is systematically adjusted for the upcoming vowel in apparent support of a planned response. However, when the task is viewed from a physiological perspective a simpler interpretation is possible that does not rely on a complicated anticipatory or look-ahead (explicit planning) mechanism operating at select

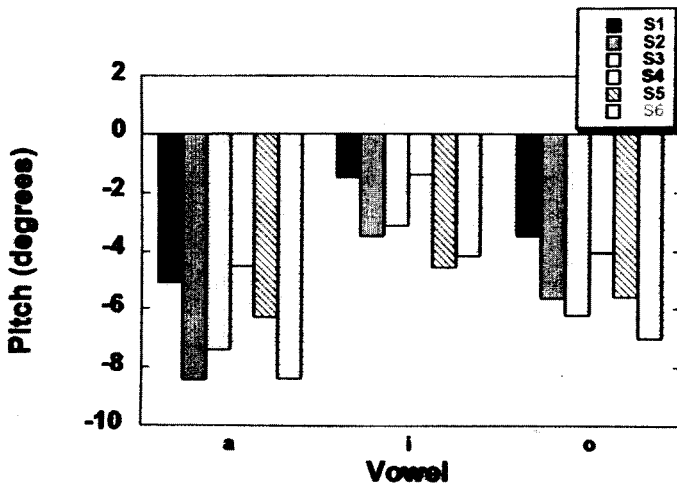


Figure 1. The pitch of the jaw (in degrees relative to the occlusal plane) averaged across the initial consonants /s/, /t/, /f/, and /k/ in a CVC context for six subjects plotted as a function of the medial vowel.

times during production. For almost all consonants and vowels the jaw is activated to position the constriction-producing articulators, in particular the tongue and lips. The muscles involved in positioning the mandible for different syllable-initial consonants and those involved in the production of many of the vowels overlap considerably. One of the characteristics of speech production is the continuous and overlapping nature of the process such that activations for contiguous phonetic gestures are not discrete in time. As such, it is more likely that commands for a syllable-initial consonant and the following vowel overlap in time. Given that the C and following V share some of the same musculature, and hence motoneuron pools, summation would occur and create small but systematic shifts in the consonant-specific spatial positioning of the mandible due to the upcoming vowel. Only by considering potential biomechanical interactions, and explanations of observable phenomena at a physiological level can the control principles and properties of the speech motor control system be realistically interpreted.

SPEECH PRODUCTION UNITS AND THEIR CONTROL

The speech production process, like most functional human behaviors, relies on units of action. From a neurobiological perspective there are a number of potential candidate constructs that may be used in describing the units of action. Two of these, the reflex and fixed action patterns, appear to lack the necessary flexibility to capture the adaptive nature of speech production. In contrast, the concept of functional synergies (Bernstein, 1967), and its elaboration, the coordinative structure (Easton, 1972; Turvey, 1977; Fowler et al., 1980;

Kelso, 1986; Saltzman, 1986), appear to reflect more closely an organizational principle for speech production. While it is clear that coordinative structures, comprised of linguistically-significant gestures, are units of action, it does not necessarily follow that they reflect a distinct level of neural control for speech motor actions. Rather, based on considerations of intergestural resistance to perturbation (Munhall et al., 1994; Löfqvist & Gracco, 1991) and the functional requirements for sound production, it has been suggested that the lowest level of neural control for speech is something on the order of gestural constellations or vocal tract configurations that map onto the phones of the language (see Browman & Goldstein, 1986; 1992; this volume; Gracco, 1990; 1991; Gracco & Löfqvist, 1994). The neuromotor patterns for speech, then, are viewed as characteristic ways of manipulating the vocal tract and are coded according to overall vocal tract goals.

It is also of considerable importance to understand the goal level organization for speech in terms of vocal tract targets and associated control. The concept of spatial targets for speech was suggested by Lashley (1951) in discussing space coordinate systems for controlling serial movements such as those for speech. In spite of the intuitive appeal of speech motion being planned in a spatial reference frame, the notion of spatial targets for speech has received little attention. One reason for the limited attention, again, appears to be related to the presence of variability in the observable signal in which variable vocal tract shapes yield acceptable acoustic signals (cf. Ladefoged et al., 1972). Explanations for the variability range from noise in the system (Perkell, 1990) to systematic adjustments that assure goal acquisition (Gracco & Abbs, 1986; Perkell et al., 1995). These positions rest on a number of assumptions regarding the control of speech movements, the degree of control precision and the goals for speech. The spatial variability that characterizes speech motion can be interpreted as reflecting loosely specified goals in an abstract task space (Abbs et al., 1984; Saltzman, 1986). That is, the details of a task are only specified in a general sense with mechanisms available to assure accurate production. In the present conceptualization, the accuracy is achieved through the integration of somatic sensory afferents and stored central motor commands. An issue of some importance, then, is the amount of variation that can be tolerated in the output. A general perspective can be obtained from consideration of the structure and function of the human nervous system as an information processing device. As pointed out by von Nuemann (1958), the nervous system is an analog device that is ideally suited for reliable operation, not precision. In this context it can be suggested that articulatory performance is good enough without incurring excessive "costs" (Nelson, 1983) with the degree of precision inherently dependent on the listener's ability to extract meaning from the speech code. A recent, conceptually attractive perspective has been offered by Guenther (1994) in which spatial targets for speech are viewed as regions rather than points (convex hulls) in orosensory space. While the available data is limited it is difficult to imagine that speech is not planned to some extent in a spatial coordinate frame since inappropriately placed articulators will produce seriously compromised sounds. Moreover, there is a certain mapping that exists between constriction locations and degrees, and the notion of spatial targets. An example of the apparent looseness in the precision of articulatory control can be found in recent simulation

and synthesis results reported by Gay, Bøe and Perrier (1992). Parametric manipulation of vocal tract cross sectional area and constriction location was used to determine the acoustic and perceptual boundaries of certain isolated vowels. It was shown that the formants for each of the vowels were more sensitive to changes in cross sectional area than constriction location. Vowel perception, however, was insensitive to both manipulations. From these results it was concluded that the speech production mechanism has "...considerable latitude..." in specifying the articulatory targets.

The data presented in Figure 2 support notions of loosely specified spatial goals and a relatively tolerant control system. Shown are average front and rear tongue paths obtained electromagnetically for productions of the nonsense utterances "aka", "aska", "aksa," and "asa." The asterisks placed over the rear tongue path indicate the maximum tongue height associated with the production of the /k/ in each of the nonsense words. It can be seen that the spatial position of maximum tongue height varies considerably. While the variation is systematic it is clear that the spatial position of the tongue path for /k/ is not precisely specified. Rather, the distribution of tongue positions in the different contexts supports a level of spatial precision or positioning that is best described as stochastic. Other kinematic data reported by Perkell and colleagues (Perkell, 1990; Perkell & Nelson, 1982; Perkell & Cohen, 1989) are also consistent with a relaxed degree of articulatory control.

SENSORY-BASED MOVEMENT ADJUSTMENTS

The conceptualization of stored central commands that represent vocal tract configurations as units of speech motor action requires an adaptive mechanism or process that can adjust the commands to context.

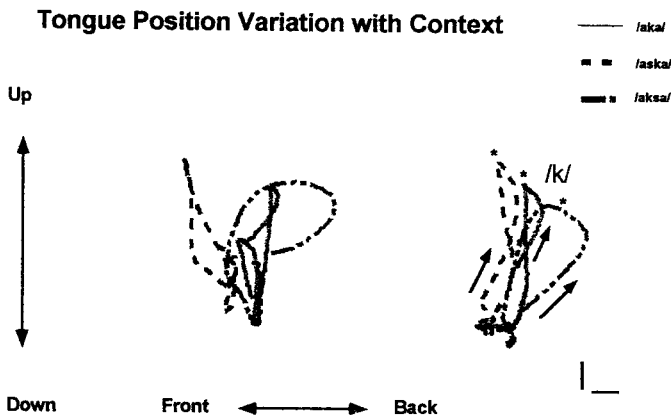


Figure 2. Changes in the point of constriction for the rear of the tongue for /k/ associated with different contexts. Arrows reflect the path of motion for the four contexts. Calibration bars represent 5 mm.

For example, generating a similar set of central commands for a /t/ before a high versus a low vowel will not produce the same desired result, namely, contact with the alveolar ridge. Therefore, some mechanism must be available to adjust the stored commands to changes in the peripheral state of the vocal tract. As argued elsewhere, (Abbs et al., 1984; Gracco, 1987; 1990; 1991; 1995; Saltzman & Munhall, 1989), real-time adaptations to central commands can be easily accomplished through the integration of sensory information. Human and nonhuman studies have shown that sensory receptors located throughout the vocal tract are sufficient to provide a range of dynamic and static information which can be used to signal position, speed, and location of physiological structures on a movement to movement basis (cf. Munger & Halata, 1983; Dubner et al., 1978 for reviews). Studies utilizing perturbation of speech motor output indicate that the rich supply of orofacial somatic sensory afferents interacting with central motor commands have the requisite properties to yield the flexible speech motor patterns involved in oral communication (Abbs & Gracco, 1984; Gracco & Abbs, 1985; Gracco & Abbs, 1988; Kelso et al., 1984).

A schematic of the general manner in which sensorimotor interactions may occur is presented in Figure 3. What is being depicted is a simplified representation of sensory and motor spaces within the nervous system. No attempt has been made to represent the specific anatomical locations of the sensory and motor spaces. Rather, the spaces are a lumped representation of brain stem, subcortical and cortical regions. Structurally, there is strong evidence for the interaction of sensory information from receptors located within the vocal tract with speech motor output at many if not all levels of the neuraxis (cf. Gracco, 1987; Gracco & Abbs, 1987; Barlow & Farley, 1989 for a summary of the vocal tract representation in multiple cortical and subcortical sensory and motor regions).

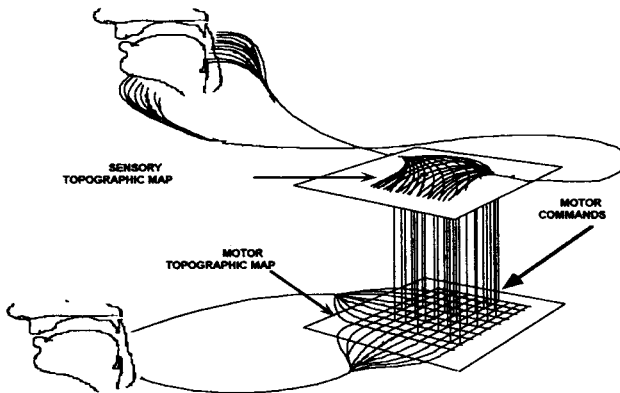


Figure 3. A scheme depicting one possible means of on-line modifications of stored central motor commands resulting from real-time changes in the vocal tract periphery. Topographic somatic sensory information continuously deforms the sensory state space which in turn modifies a topographic representation of the vocal tract in motor state space. The output of the motor space is directed to brain stem motor centers controlling the vocal tract. (Modified from Churchland, 1989).

Further, brain stem organization, evidenced by reflex studies, demonstrates a range of complex interactions in which sensory input from one structure such as the jaw or face is potentially able to modify motor output from other orofacial and lingual regions (Dubner et al., 1978; Smith et al., 1985; Weber & Smith, 1987). A summary of the specific receptor types within the vocal tract can be found in Dubner, Sessle and Storey (1978) and Kent, Martin and Suffit (1990).

It is suggested that as the peripheral conditions change during speaking, the sensorimotor connections continuously change the state of the various motor output regions subserving speech. As such, the same set of central commands for producing a /t/ will have different effects when impinging on a motor region that has been conditioned by a low jaw position compared to a high jaw position associated with the preceding vowel. The speech motor control system apparently adjusts for these movement-to-movement variations by incorporating somatic sensory information from the various muscle and mechanoreceptors located throughout the vocal tract. Sensorimotor connections allow the central commands to be sensitive to a constantly changing peripheral environment in a predictive manner (Gracco & Abbs, 1987; Gracco, 1987). Given the latencies previously reported (50-100 msec; Abbs & Gracco, 1984) and the time necessary for using predictive estimates (based on velocity and/or acceleration) of the dynamic peripheral conditions, it has been suggested that speech motor commands can be updated in real-time from somatic sensory receptor information (Gracco, 1987). That is, during even the most rapid speaking conditions, there is sufficient time available to make simple coordinate transformations between somatic sensory and motor states allowing for continuous modification of descending motor commands. Both empirical and theoretical considerations suggest that somatic sensory interaction is one plausible method to achieve flexibility from relatively stereotypic central motor commands (Gracco, 1987; Gracco, 1990).

A consequence of this conceptualization is that any novel event (the onset of a stuttering episode, for example) or any neurological sequela that change speech motor output parameters will change the sensorimotor environment, such that the same central motor commands will produce different (and possibly maladaptive) vocal tract motion. For example, the onset of a stuttering event, whether movement repetition, prolongation or hesitation, has somatic sensory consequences in which the afferent input onto motor regions will change the overall level of excitability. As a result, the same set of central commands presented to areas associated with speech motor output will result in deviant output until the speech production process is reset in some manner. The fact that it is not easy for an individual who stutters to reset the production process probably reflects the difficulty of on-line modification of sequential central commands for speech and the automatic nature of the speech production process. For neurological disorders such as Parkinson's disease, cerebellar disease, or motor aphasia, there are a myriad of changes that result from the neurological damage that would result from changes in the central commands themselves. Some potential consequences associated with certain movement disorders will be discussed later.

SEQUENCING OF SPEECH MOTOR ACTIONS

Speech is more than the specification of characteristic motor patterns coded to produce vocal tract configurations adjusted for context. An important consideration in speech production is the sequencing of vocal tract actions into communicatively meaningful units of production. An important theoretical issue is determining how the nervous system integrates speech production units into coherent packages for information transfer. As pointed out by Lashley (1951), serial actions such as those for speech, locomotion, typing and the playing of musical instruments cannot be explained in terms of successions of external reflexes. Rather the apparent rhythmicity found in all but the simplest motor activities suggests that some sort of temporal patterning may form the foundation for motor as well as perceptual activities. A number of observations are consistent with the presence of some kind of rhythm generating mechanism 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; Saltzman et al., 1991; Saltzman et al., 1995; Saltzman et al., 1992). Other results such as minimal movement durational changes from static (Lindblom et al., 1987) and dynamic perturbation (Gracco & Abbs, 1988) and durational consistencies across experimental sessions (Kozhevnikov & Chistovich, 1965) are consistent with an underlying mechanism in which sequential timing is maintained. However, a strictly isochronous mechanism is not plausible given the different durational requirements for consonants and vowels. Classes of sounds appear to have certain intrinsic temporal properties (or constraints) which must interact with any proposed suprasegmental timing mechanism. 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. High pressure consonants often show faster movements than their voiced low pressure counterparts. It has been suggested that a central rhythm generator provides the timing framework for the sequencing of production units and the general intrinsic requirements of the units in turn modulate the instantaneous frequency of the oscillator such that speech movement timing can be represented as an interaction between extrinsic and intrinsic mechanisms (Gracco, 1990; 1991; 1994).

An important consequence of incorporating a central rhythm generator into a speech production model is the ability to explain rate, stress, and final lengthening changes with manipulation of a single mechanism: global (over the course of an utterance) and local (phone and syllable level) changes in rhythmic frequency. Moreover, the rhythmic nature of the output is potentially available to facilitate speech perception by making signal stream segmentation more predictable (Cutler & Mehler, 1993; Lashley, 1951; Martin, 1972). The rhythmic modulation of speech production would provide the perceptual system with a predictable framework for sampling and parsing the output. The breakdown in the rhythmic structure of speech associated with a number of different speech motor disorders (Kent & Rosenbek, 1982) and the pervasive rhythmicity found throughout the nervous system (Llinas,

1986; Llinas, 1991) strongly suggests that the underlying rhythm is a network property rather than a property of a specific neuroanatomical location.

NEURAL SUBSTRATE

It has been known for over 100 years that multiple regions of the brain are involved in some manner in producing speech and language. The neural substrate for speech has been identified from a variety of sources including human mapping studies using electrical stimulation (Penfield & Roberts, 1959; Ojemann, 1983; Mateer, 1983), positron emission tomography (Petersen et al., 1989; Wise et al., 1991; Petersen & Fiez, 1993), functional magnetic resonance imaging (McCarthy et al., 1993; Shaywitz et al., 1995; Pugh et al., in press) and neuroanatomical studies of nonhuman primates (Muakassa & Strick, 1979; Woolsey et al., 1952). A number of cortical and subcortical regions have been identified in which a representation of the vocal tract can be found (see Barlow & Farley, 1989; Gracco & Abbs, 1987; Kimura, 1993 for reviews). Cortical regions with vocal tract representations include the primary motor and sensory areas (MI and SI, respectively), the so-called nonprimary motor areas including supplementary motor area (SMA) and premotor area (PM; lateral precentral cortex), and a posterior parietal region. The general PM area and posterior parietal regions (including portions of the temporal region in man) comprise the areas associated with Broca's and Wernicke's areas respectively (Penfield & Roberts, 1959; Kimura, 1993). Extensive subcortical representations can also be found in the cerebellar cortex, deep cerebellar nuclei and regions of the basal ganglia.

An interesting aspect of these representations is their extrinsic (and generally reciprocal) interconnections. For example, the different cortical areas are connected to different subcortical structures and contain projections from or project to distinct and (relatively) non-overlapping regions of the thalamus. The PM area receives input from the deep cerebellar nuclei via the thalamus and projects to the primary motor area (MI) as well as contributing direct descending projections to brain stem nuclei. Similar segregated extrinsic connections are found for regions of the basal ganglia and SMA. In addition, SI projects to posterior parietal regions which in turn project to the motor, premotor and temporal regions with descending projections to brain stem nuclei. A summary of neuroanatomical data reported by Schell and Strick (1984) suggests that large regions of the cortex and subcortex are interconnected and maintain relatively segregated modules that ultimately converge at the output. These diverse neural areas, which represent large regions of the nervous system, display an extrinsic organization consistent with the concept of neural modules hypothesized by Mountcastle, suggesting distributed processing functions (Mountcastle, 1978). It should be noted that these large scale networks all have access to peripheral sensory information from somatic receptors as well as the visual and auditory receptors and therefore display "reentrant" characteristics, with changes in one system allowing changes or readjustment in all convergent systems (Edelman, 1987). While this overview leaves out much detail it can be seen that the neuroanatomy underlying speech and language is quite complex and highly

specialized to receive, integrate and act on the external and internal environment of the organism.

An additional source of insight into the nervous system organization for speech and language comes from neurological disorders. From a synthesis of various observations some general conclusions can be drawn. A surprising characteristic of almost all lesions involving the central nervous system is the accompaniment of motor impairments with cognitive or linguistic impairments and the converse. It appears, as suggested by Jackson (1875), that the so-called higher centers of the nervous system may be extensions of the lower nervous centers which represent impressions and movements. Consistent with the neuroanatomical substrate outlined above, damage to the cerebellum and/or PM area often results in impairments similar at least in acoustic and perceptual respects (Kent & Rosenbek, 1982). Damage to either of these regions often produces a breakdown in speech that can be characterized as a disruption of the smooth timing of sequential speech movements. Cerebellar patients often show a decomposition of movement, as though the various parts of a complex movement had to be thought out one by one (Holmes, 1922). Dysmetria is also a characteristic of cerebellar damage suggesting that the ability to integrate sensory information to produce appropriately calibrated actions has been affected. These symptoms are generally consistent with those associated with Broca's aphasia (due to anterior premotor lesions). For example, electrical stimulation of the PM area, which receives output from the deep cerebellar nuclei via the thalamus, causes speech arrest (Penfield & Roberts, 1959) and an inability to sequence multiple speech movements (Mateer, 1983). The contribution of the cerebellum to the control of movement is undergoing some modification. While the cerebellum is often considered a motor center, there are multiple sources of relatively new data to suggest that it is also involved in a variety of other behaviors that require more than just motor activities (see Gao et al., 1996 for review). However, it should be remembered that all behaviors are sensorimotor in nature. As such, the cerebellum and the projections to Broca's areas may be appropriately regarded as sensorimotor integration areas in which central commands are modified before the final output. As a module that integrates sensory information on a task-specific basis, the role of the cerebellum and Broca's area appears to be to assist in matching task-specific motor commands to the periphery and the task requirements. The task requirements for communication reflect the phonetic context of the linguistic structure. Because these systems operate together, damage to either produces similar effects that would consist of problems with sequencing successive vocal tract states and adjusting central commands to changes in the peripheral environment.

A similar situation exists for impairments associated with basal ganglia and SMA damage. It is well known that prior to movement SMA activity displays characteristics consistent with movement preparation (Tanji et al., 1980; Deecke & Kornhuber, 1978) while the basal ganglia reflect activity that is consistent with a scaling of motor commands (Horak & Anderson, 1984a, b). Basal ganglia damage, characterized by Parkinson's disease, often results in speech characterized by imprecise consonant production, mono-pitch and loudness, and articulator movements that are reduced in amplitude and speed. SMA damage, on the

other hand, results in speech impairments that are similar to and more extreme than those associated with basal ganglia damage, ranging from total speech arrest to imprecise articulation and a reduction in spontaneously generated speech (Laplane et al., 1977; Masdeu et al., 1978; Damasio & Van Hoesen, 1980). In the case of damage to either of these regions, the resulting movement deficits are consistent with a reduced level of activation that accompanies the preparation and modulation of central commands. A reduction in motor preparation and/or a reduction in scaling of motor commands would produce many of the symptoms normally associated with damage to one or the other of these related systems. For example, a lack of modulation of central commands over the course of an utterance would result in a reduction in the ability to produce the movement changes characteristic of emphatic stress (Forrest et al., 1989) and a lack of intonational changes over the course of an utterance. Moreover, a reduction in the scaling of central commands would result in rather consistent articulatory undershoot and consequent bradykinesia. From the present conceptualization, stored central commands that specify characteristic vocal tract configurations are modulated for context by somatic sensory input and scaled based on suprasegmental requirements such as those necessary to produce intonation, loudness, stress and rate manipulations. It is suggested that these neural changes operate through the basal ganglia/SMA system.

A final issue with regard to the neuromotor control of speech is the interpretation of speech movement deficits due to damage to cortical systems traditionally associated with language. The traditional cortical areas often considered to represent linguistic processes and act as the interface between language and speech are Broca's and Wernicke's areas. It has been suggested above that Broca's area, in conjunction with the deep cerebellar nuclei, is involved in the sensorimotor adjustment and timing of segmental phonetic units. Consistent with this position are aphasic data and the theoretical position outlined by Kimura (1993). Kimura (1993) suggests that aphasic patients with anterior lesions have reduced syllable-level fluency (i.e., difficulty with sequencing vocal tract configurations). In contrast, aphasic patients with posterior lesions have difficulty with sequencing syllables into larger multisyllables. Moreover, patients with damage to the posterior speech areas also display output impairments that appear to reflect inappropriate phonological selection compared to the more phonetic errors exhibited by anterior aphasics (Blumstein, 1981). Thus, there are apparently some general functions associated with the hypothetical distributed processing modules known to represent and support motor speech production.

SUMMARY

A conceptual model of speech production has been outlined that provides a framework for investigating the neuromotor characteristics of fluent speech. As noted above, speaking is a communicative act in which the output represents a synthesis of potentially independent but mutually overlapping processes. The processes overlap in time and each stage of the output reflects, to some extent, the influence of any or all contributing levels. Whether one views

the communicative process as serial or parallel (or some combination), articulation represents the synthesis of cognitive, linguistic and sensorimotor processes (Levelt, 1989; Bock & Levelt, 1994; Jescheniak & Levelt, 1994). In order to understand and predict this complex process the basic components and the manner in which they interact must be made explicit. In the preceding, an attempt has been made to identify the basic components and properties of a speech production model and the manner in which they might interact to instantiate the communication process.

Summarized in Figure 4 is a schematic representation of the fundamental processes and their interactions hypothesized to underlie the production of fluent speech. A primary component of the speech production process is the preparation of the sensorimotor system for activation. That is, excitability levels associated with sensory and motor regions are increased in a general sense and specific regions involved with communication are tuned for the upcoming motor commands. The overall levels of excitability are dependent on certain pragmatic requirements (emotional content, speaking rate, noisy environment, etc.) that will determine in a general sense the overall level of effort. The stored configurations, which include neural commands that specify the coordination among their gestural components, converge on and interact with the preparatory activations on output areas. The central commands that give rise to specific and neuroanatomically focused motor patterns result in a movement-to-movement tuning of the motor output structures in characteristic ways consistent with the articulatory organization for unique vocal tract configurations. The motor state space is also conditioned by ongoing topographic projections from somatic sensory vocal tract representations which have been made active by the preparatory process.

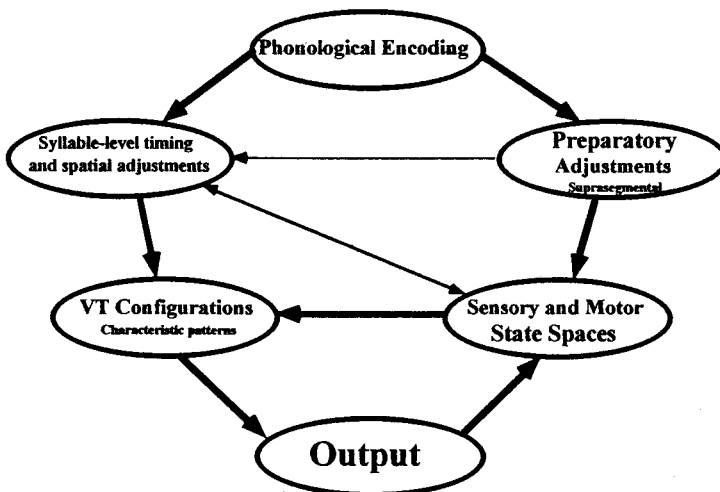


Figure 4. A schematic model of hypothetical speech motor processes. The thickness of the lines reflects the strength of the connections; double headed arrows represent interactive connections. See text for details.

The speech motor system receives input in the form of a phonological code specifying, among other things, the sequence of characteristic neuromotor patterns associated with vocal tract configurations unique for each phone of the language.

At the level of the phonological encoding process the unit of organization is larger than individual phonetic gestures. A level of organization, on the order of a syllable, which may contain one or more phonetic gestures, is hypothesized. This syllable level temporal organization forms the rhythmic basis for all higher level (suprasegmental) temporal phenomena. It is further hypothesized that the rhythmic organization reflects a system property rather than a manifestation of a single rhythmic or oscillatory source. The phonetic composition of each syllable adjusts the instantaneous frequency of the output but does not reset the rhythm. The frequency characteristics of the oscillator can be easily modified by simple tonic inputs as part of the preparatory process that can increase or decrease speaking rate.

In keeping with one of the constraints discussed at the outset, these processes appear to be consistent with known (or inferred) nervous system functions. The motor preparation process involves the SMA/basal ganglia network in which cortical and subcortical sensory and motor areas are activated in preparation for action and tuning the sensorimotor centers in ways that reflect a time scale involving utterance-level and possibly suprasegmental adjustments. It should be noted that while this process may be thought of as motor, it is dependent on the communicative requirements of the situation and involves setting up sensory as well as motor consequences. Hence, all functional speech processes are both sensorimotor and communicative and reflect a synthesis of all available levels of organization. The phonological encoding process involves structures that impart meaning, perhaps lexical items, that are parsed into multisyllabic phonetic codes that are executed on a syllable by syllable basis. In concert with Broca's area, the cerebellar nuclei adjust the spatiotemporal characteristics of the motor commands for sequencing within a syllable and adjust the overall rhythmicity of the system based on phonetic context. The cerebellum has extensive connections onto almost all regions of the nervous system to allow it to play an executive role in sensorimotor integration and motor command adjustment (Arshavsky et al., 1985). Moreover, in contrast to the general setting of sensorimotor excitability levels associated with the SMA/basal ganglia system, the cerebellar/PM system appears to be involved in more specific changes associated with contextual adjustments of motor commands. Hence, it can be suggested that damage to this system will result in a breakdown in the sequencing of successive phonetic gestures, articulatory undershooting as well as overshooting and increased levels of noise or movement variability while damage to the SMA/basal ganglia system will predominantly result in undershooting, decreased speaking rate, a lack of task-specific modulation and a decrease in variability.

The model rests on a number of assumptions about nervous system function and associated organizational principles that, while specific to speech production, may generalize to many other behaviors. First, the level of control for speech is minimally at a level that reflects the smallest functional unit of speech, linguistically-significant vocal tract configurations. These

units are ultimately organized into larger units that ultimately represent the communicative function of the task. This conceptualization suggests that speech production is a nested process with function as the organizing principle at each level. Speech movements are contextually variable suggesting that vocal tract configurations for the phonetic segments are only loosely specified reflecting the redundancy of cues available to extract meaning. A fundamental principle that emerges is that the organization for speech and language operates at multiple levels in parallel with communication a synthetic and stochastic process. As a result no one movement component or signal attribute or neural structure is solely responsible for information transfer; the neural control of speech relies on flexible processes and reliable performance rather than invariant principles and rigid tolerances. Finally, a theoretical perspective that focuses on explanations at the level of the anatomy, physiology and fundamental nervous system processes, makes it possible to generate a parsimonious and neurobiologically-plausible model of speech production, in which simple functions interact to produce complex patterns.

ACKNOWLEDGMENTS

Supported by research grant numbers RO1 DC 00595 and P50 DC 00121 from the National Institute on Deafness and Other Communication Disorders, National Institutes of Health.

REFERENCES

- Abbs, J.H., & Gracco, V.L. (1984). Control of complex motor gestures: Orofacial muscle responses to load perturbations of the lip during speech. *Journal of Neurophysiology*, *51*(4), 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.
- Barlow, S.M., & Farley, G.R. (1989). Neurophysiology of speech. In D.P. Kuehn, M.L. Lemme, & J. Baumgartner (Eds.), *Neural bases of speech, hearing, and language* (pp. 146-200). Boston: College-Hill Press.
- Bernstein, N. (1967). *The co-ordination and regulation of movements*. New York: Pergamon Press.
- Blumstein, S.E. (1981). Neurolinguistic disorders: Language-brain relationships. In S.B. Filskov, & T. J. Boll (Eds.), *Handbook of Clinical Neuropsychology*. New York: Wiley.
- Browman, C.P., & Goldstein, L. (1986). Towards an articulatory phonology. *Phonology Yearbook*, *3*, 219-252.
- Browman, C.P., & Goldstein, L. (1992). Articulatory phonology: An overview. *Phonetica*, *49*(3-4), 155-180.
- Churchland, P.S. (1986). *Neurophilosophy: Toward a unified science of the mind-brain*. Cambridge: MIT Press.
- Churchland, P.M. (1989). *A neurocomputational perspective: The nature of mind and the structure of science*. Cambridge: MIT Press.
- Cutler, A., & Mehler, J. (1993). The periodicity bias. *Journal of Phonetics*, *21*, 103-108.
- Damasio, A.R., & Van Hoesen, G.W. (1980). Structure and function of the supplementary motor area. *Neurology*, *30*, 359.

- Deecke, L., & Kornhuber, H.H. (1978). An electrical sign of participation of the mesial 'supplementary' motor cortex in human voluntary finger movement. *Brain Research*, *159*, 473-476.
- Dubner, R., Sessle, B.J., & Storey, A.T. (1978). *The neural basis of oral and facial function*. New York: Plenum Press.
- Easton, T.A. (1972). On the normal use of reflexes. *American Scientist*, *60*, 591-599.
- Edelman, G.M. (1987). *Neural Darwinism*. New York: Basic Books, Inc.
- Forrest, K., Weismer, G., & Turner, G.S. (1989). Kinematic, acoustic, and perceptual analyses of connected speech produced by Parkinsonian and normal geriatric adults. *Journal of the Acoustical Society of America*, *85*, 2608-2622.
- 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.
- Gao, J.-H., Parsons, L., Bower, J., Xiong, J., Li, J., & Fox, P. (1996). Cerebellum implicated in sensory acquisition and discrimination rather than motor control. *Science*, *272*, 545-547.
- Gay, T., Bøe, L.-J., & Perrier, P. (1992). Acoustic and perceptual effects of changes in vocal tract constrictions for vowels. *Journal of the Acoustical Society of America*, *92*, 1301-1309.
- Garrett, M. (1991). Disorders of lexical selection. In W.J.M. Levelt (Ed.). *Lexical access in speech production* (pp. 143-180). Cambridge, MA: Blackwell.
- Gracco, V.L. (1987). A multilevel control model for speech motor activity. In H. Peters, & W. Hulstijn (Eds.), *Speech motor dynamics in stuttering* (pp. 57-76). Berlin: 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. Hammond (Ed.), *Cerebral control of speech and limb movements* (pp. 3-28). North Holland: Elsevier.
- Gracco, V.L. (1991). Sensorimotor mechanisms in speech motor control. In H. Peters, W. Hulstijn, & C.W. Starkweather (Eds.), *Speech motor control and stuttering* (pp. 53-78). North Holland: Elsevier.
- Gracco, V.L. (1994). Some organizational characteristics of speech movement control. *Journal of Speech and Hearing Research*, *37*, 4-27.
- Gracco, V.L. (1995). Central and peripheral components in the control of speech movements. In Bell-Berti, F., & Raphael, L. (Eds.), *Producing speech: Contemporary issues for Katherine Safford Harris* (pp. 417-432). Woodbury: AIP Press.
- Gracco, V.L., & Abbs, J.H. (1985). Dynamic control of perioral system during speech: Kinematic analyses of autogenic and nonautogenic sensorimotor processes. *Journal of Neuroscience*, *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. (1987). Programming and execution processes of speech movement control: Potential neural correlates. In E. Keller & M. Gopnik (Eds.), *Symposium on motor and sensory language processes* (pp. 163-201). New Jersey: Lawrence Erlbaum Associates, Inc.
- 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, A. (1994). Speech motor coordination and control: Evidence from lip, jaw, and laryngeal movements. *Journal of Neuroscience*, *14*, 6585-6597.

- Guenther, F.H. (1994). A neural network model of speech acquisition and motor equivalent speech production. *Biological Cybernetics*, 73, 43-53.
- Ho, T.P., Azar, K., Weinstein, S., & Bowley, W.W. (1982). Physical properties of human lips: Experimental and theoretical analysis. *Journal of Biomechanics*, 15, 859-866.
- Holmes, G. (1922). Clinical symptoms of cerebellar disease and their interpretation. The Croonian lectures I. *Lancet*, 1, 1177-1182.
- 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.
- Jackson, J.H. (1875). *Clinical and physiological researches on the nervous system*. London: Churchill.
- Kelso, J.A.S. (1986). Pattern formation in speech and limb movements involving many degrees of freedom. In H. Heuer, & C. Fromm (Eds.), *Generation and modulation of action patterns* (pp. 105-128). Berlin: Springer-Verlag.
- Kelso, J.A.S., Tuller, B., V.-Bateson, E., & Fowler, C.A. (1984). Functionally specific articulatory cooperation following jaw perturbations during speech: Evidence for coordinative structures. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 812-832.
- Kent, R.D., & Rosenbek, J.C. (1982). Prosodic disturbance and neurologic lesion. *Brain and Language*, 15, 259-291.
- Kent, R.D., Martin, R.E., & Sufit, R.L. (1990). Oral sensation: A review and clinical prospective. In H. Winitz (Ed.), *Human communication and its disorders* (pp. 135-191). Norwood, NJ: Ablex Publishing.
- Kimura, D. (1993). *Neuromotor mechanisms in human communication*. New York: Oxford University Press.
- Kozhevnikov, V., & Chistovich, L. (1965). *Speech: Articulation and perception*. Joint Publications Research Service, 30,453; U.S. Department of Commerce.
- Laboissière, R. Ostry, D., & Feldman, A. (1996). Control of multi-movement systems: Human jaw and hyoid movements. *Biological Cybernetics*, 74, 373-384
- Ladefoged, P., DeClerk, J., Lindau, M., & Papcun, G. (1972). An auditory-motor theory of speech production. *UCLA Working Papers in Phonetics*, 22, 48-75.
- Laplante, D., Talairach, J., Meininger, V., Bancaud, J., & Orgogozo, J.M., (1977). Clinical consequences of corticectomies involving the supplementary motor area in man. *Journal of the Neurological Sciences*, 34, 301-314.
- Lashley, K.S. (1951). The problem of serial order in behavior. In L.A. Jeffress (Ed.), *Cerebral mechanisms in behavior: The Hixon symposium*. New York: Wiley.
- Levelt, W.J.M. (1989). *Speaking: from intention to articulation*. Cambridge, MA: MIT Press.
- Levelt, W.J.M. (1992). Accessing words in speech production: Stages, processes and representations. *Cognition*, 42, 1-22.
- Lindblom, B., Lubker, J., Gay, T., Lyberg, P., Branderal, P., & Holgren, K. (1987). The concept of target and speech timing. In R. Channon, & L. Shockery (Eds.), *In honor of Ilse Lehiste* (pp. 161-181). Dordrecht, The Netherlands: Foris Publications.
- Llinas, R.R. (1986). Neuronal oscillators in mammalian brain. In M. J. Cohen & F. Strumwasser (Eds.), *Comparative neurobiology: Modes of communication in the nervous system*. (pp. 279-290). New York: Wiley.
- Llinas, R.R. (1991). The noncontinuous nature of movement execution. In D.R. Humphrey, & H.-J.

- Freund, (Eds.), *Motor control: Concepts and issues*. (pp. 223-242). New York: Wiley.
- Löfqvist, A., & Gracco, V.L. (1991). Discrete and continuous modes in speech motor control. *PERILUS*, XIV, 27-34.
- Lynn, A.M.J., & Yemm, R. (1971). External forces required to move the mandible of relaxed human subjects. *Archives of Oral Biology*, 16, 1443-1447.
- Martin, J.G. (1972). Rhythmic (hierarchical) versus serial structure in speech and other behavior. *Psychological Review*, 79, 487-509.
- Masdeu, J.C., Schoene, W.C., & Funkenstein, H. (1978). Aphasia following infarction of the left supplementary motor area: A clinicopathologic study. *Neurology*, 28, 1220-1223.
- Mateer, C.A. (1983). Motor and perceptual functions of the left hemisphere and their interactions. In S. J. Segalowitz (Ed.), *Language functions and brain organization* (pp. 145-170). New York: Academic Press.
- McCarthy, G., Blamire, A.M., Rothman, D.L., Gruetter, R., Shulman, R.G. (1993). Echo-planar magnetic resonance imaging studies of frontal cortex activation during word generation in humans. *Proceedings of the National Academy of Sciences*, 89, 5675-5679.
- Mountcastle, V.B. (1978). An organizing principle for cerebral function: The unit module and the distributed system. In G.M. Edelman, & V.B. Mountcastle, (Eds.), *The mindful brain: Cortical organization and the group-selective theory of higher brain function* (pp. 7-50). Cambridge: MIT Press.
- Muakassa, K.F., & Strick, P.L. (1979). Frontal lobe inputs to primate motor cortex: evidence for four somatotopically organized "premotor" areas. *Brain Research*, 177, 176-182.
- Munhall, K., Löfqvist, A., & Kelso, J.A.S. (1994). Lip-larynx coordination in speech: effects of mechanical perturbations to the lower lip. *Journal of the Acoustical Society of America*, 96, 3605-3616.
- Nelson, W.L. (1983). Physical principles for economies of skilled movements. *Biological Cybernetics*, 46, 135-147.
- Ojemann, G.A. (1983). Brain organization for language from the perspective of electrical stimulation mapping. *The Behavioral and Brain Sciences*, 6, 189-230.
- Ostry, D.J., Gribble, P.L., & Gracco, V.L. (1996). Coarticulation of jaw movements in speech production: Is context sensitivity in speech kinematics centrally planned? *Journal of Neuroscience*, 16, 1570-1579.
- Penfield, W., & Roberts, L. (1959). *Speech and brain mechanisms*. Princeton, N. J.: Princeton Univ. Press.
- Perkell, J.S. (1990). Testing theories of speech production: Implications of some detailed analyses of variable articulatory data. In W. Hardcastle, & A. Marchal, (Eds.) *Speech production and speech modeling*, (pp. 263-288). Dordrecht: Kluwer.
- Perkell, J.S. & Nelson, W.L. (1982). Articulatory targets and speech motor control: A study of vowel production. In S. Grillner, A. Persson, B. Lindblom, & J. Lubker, (Eds.), *Speech motor control* (pp. 187-204). Oxford: Pergamon.
- Perkell, J.S. & Cohen, M.H. (1989). An indirect test of the quantal nature of speech in the production of the vowels /i/, /a/ and /u/. *Journal of Phonetics*, 17, 123-133.
- Perkell, J.S., Matthies, M.L., Svirsky, M.A., & Jordan, M.I. (1995). Goal-based speech motor control: A theoretical framework and some preliminary data. *Journal of Phonetics*, 23, 23-35.
- Petersen, S.E., & Fiez, J.A. (1993). The processing of single words studied with positron emission tomography. *Annual Review of Neuroscience*, 1, 509-530.
- Petersen, S.E., Fox, P.T., Posner, M.I., Mintun, M., & Raichle, M.E. (1989). Positron emission tomographic studies of the processing of single words. *Journal of Cognitive Neuroscience*, 1, 153-170.

- Pugh, K., Shaywitz, B.A., Shaywitz, S.E., Fulbright, R.K., Byrd, D., Skudlarski, P., Shankweiler, D.P., Katz, L., Constable, R.T., Fletcher, J., Lacadie, C., Marchione, K., & Gore, J.C. (in press) Auditory selective attention: An fMRI investigation. *NeuroImage*.
- Saltzman, E.L. (1986). Task dynamic coordination of the speech articulators: A preliminary model. In H. Heuer, & C. Fromm, (Eds.), *Generation and modulation of action patterns* (pp. 129-144). Berlin: Springer-Verlag.
- Saltzman, E.L., & Munhall, K.G. (1989). A dynamical approach to gestural patterning in speech production. *Ecological Psychology, 1*, 333-382.
- Saltzman, E., Kay, B., Rubin, P., & Kinsella-Shaw, J. (1991). Dynamics of intergestural timing. *Perilus XIV*, 47-56, Institute of Linguistics, University of Stockholm, Stockholm, Sweden.
- Saltzman, E., Löfqvist, A., Kinsella-Shaw, J., Kay, B., & Rubin, P. (1995). On the dynamics of temporal patterning in speech. In F. Bell-Berti, & L. Raphael, (Eds.), *Producing speech: Contemporary issues for Katherine Safford Harris*. (pp. 469-488). Woodbury, NY: American Institute of Physics.
- Saltzman, E., Löfqvist, A., Kinsella-Shaw, J., Rubin, P.E., & Kay, B. (1992). A perturbation study of lip-larynx coordination. In *Proceedings of the 1992 International Conference on Spoken Language Processing (ICSLP '92): Addendum, Banff, Alberta, Canada* Edmonton, Canada: Priority Printing.
- Schell, G.R., & Strick, P.L. (1984). The origin of thalamic inputs to the arcuate premotor and supplementary motor areas. *Journal of Neuroscience, 4*, 539-560.
- Shaywitz, B., Pugh, K., Constable, T., Shaywitz, S., Bronen, R., Fullbright, R., Shankweiler, D., Katz, L., Fletcher, J., Skudlarski, P., & Gore, J. (1995). Localization of semantic processing using functional magnetic resonance imaging. *Human Brain Mapping, 2*, 149-158.
- Smith, A., Moore, C.A., Weber, C.M., McFarland, D.H., & Moon, J.B. (1985). Reflex responses of the human jaw-closing system depend on the locus of intraoral mechanical stimulation. *Experimental Neurology, 90*, 489-509.
- Stevens, K.N. (1972). On the quantal nature of speech: Evidence from articulatory-acoustic data. In E. E. David, & P.B. Denes, (Eds.), *Human communication: A unified view* (pp. 51-66). New York: McGraw-Hill.
- Stevens, K.N. (1989). On the quantal nature of speech. *Journal of Phonetics, 17*, 3-45.
- Tanji, J., Taniguchi, K., & Saga, T. (1980). Supplementary motor area: Neuronal response to motor instructions. *Journal of Neurophysiology, 43*, 60-68.
- Turvey, M.T. (1977). Preliminaries to a theory of action with reference to vision. In R. Shaw, & J. Bransford, (Eds.), *Perceiving, acting and knowing: Towards an ecological psychology*. Hillsdale: Lawrence Erlbaum.
- Von Nuemann, J. (1958). *The computer and the brain*. New Haven: Yale University Press.
- Weber, C. M., & Smith, A. (1987). Reflex responses of jaw, lip, and tongue muscles to mechanical stimulation. *Journal of Speech and Hearing Research, 30*, 70-79.
- Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E., Frackowiak, R. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain, 11*, 1803-1817.
- Woolsey, C.N., Settlage, P.H., Meyer, D.R., Spencer, W., Pinto Hamuy, T., & Travis, A.M. (1952). Patterns of localization in precentral and "supplementary" motor areas and their relation to the concept of a premotor area. *Association for Research in Nervous and Mental Disease, 30*, 238-264.