

Timing Factors in the Coordination of Speech Movements

Vincent L. Gracco

Haskins Laboratories, New Haven, Connecticut 06511

Speech movement coordination involves substantial timing adjustments among multiple degrees of muscles and movement freedom. The present investigation examined the kinematic and muscle timing adjustments associated with the production of select speech movements. For oral closing movements, the timing of the upper lip, lower lip, and jaw peak velocities were found to be tightly coupled, apparently reflecting a coordinative strategy. In contrast, oral opening movements demonstrated reduced temporal coupling and inconsistent sequencing across subjects. Overall, it appears that the temporal organization of speech movements varies with the specific movement goals. In order to evaluate the coordinative patterns for oral closing in detail, the temporal adjustments of multiple perioral muscles associated with the systematic closing peak velocity relations were examined. The relative timing of muscle onsets and peak EMG amplitudes was found to be predictably related to the peak velocity timing variations, suggesting that the motor commands are temporally scaled to generate changes in speaking conditions. It was also found that the mechanical properties of the speech articulators influence movement coordination and can be exploited to maximize movement efficiency. The systematic change in muscle timing characteristics for all synergistic muscles apparently reduces the degrees of freedom to control, thereby facilitating the coordination process.

For even simple speech gestures, multiple degrees of movement freedom must be coordinated. The rapid nature of speech movements suggests that a significant control consideration is the timing among the multiple structures. For most functional multiarticulate tasks, the nervous system apparently establishes consistent relations among movements and muscle activity of multiple structures to reduce the control complexity (Bernstein, 1967; Gel'fand et al., 1971; Turvey, 1977). Such diverse observations as constant phase relations during locomotion, consistent patterns of activation of functional synergists during postural stabilization, and invariant relations between elbow and shoulder joints demonstrate task-dependent simplifications apparently facilitating coordination (Grillner, 1975; Shik and Orlovsky, 1976; Nashner, 1977; Soechting and Lacquaniti, 1981; Lacquaniti and Soechting, 1982). In contrast to such basic motor

actions, the specific manner in which speech production relies on such simplifying strategies to facilitate coordination is not well understood.

One form of apparent speech movement invariance involves consistent timing relations across serial movements (Kent and Netsell, 1971; Kent and Moll, 1975; Tuller et al., 1982). It has been suggested that contiguous opening and closing movements for speech share similar timing characteristics with the stance and swing phases for locomotion (Tuller and Keiso, 1984). Specifically, the relative timing of opening/closing movements is maintained across changes in speaking rate (however, see Munnhall, 1985, for discussion of potential statistical artifact). In contrast to serial or sequential speech movements, the multiarticulate actions of the lips and jaw for a single action (oral closing for the production of the "p" sound) have been shown to reflect systematic timing relations characteristic of patterned motor behaviors such as locomotion and chewing (Gracco and Abbs, 1986, 1988a). Specifically, the upper lip, lower lip, and jaw peak velocities during oral closing have been shown to be consistently ordered in time and systematically adjusted with changes in movement timing. The consistent velocity timing relations were maintained following lower lip perturbation (Gracco and Abbs, 1988a), suggesting that speech movement timing involves a central patterning process reflecting a coordinative strategy to minimize the degrees of freedom to control. However, two important issues have not been addressed in previous studies: the consistency of the timing relations for different movement phases (opening vs closing) and the characteristics of the underlying muscle activity. Comparison of opening and closing movements and evaluation of the muscle activity accompanying the consistent timing relations should provide additional insight into the control and coordination of speech movements.

Materials and Methods

Motor task. Four young adults (2 male subjects, DK and SM, 2 female subjects, NV and CD) aged 20–24 years participated in the present study. Muscle activity was recorded from at least 4 orofacial muscles using intramuscular hooked-wire electrodes spaced approximately 4 mm apart. Impedances at the time of recording were generally less than 10 k Ω . For all subjects muscle activity was sampled from 2 upper lip depressor muscles—orbicularis oris superior (OOS) and depressor anguli oris (DAO)—and 2 lower lip elevators—orbicularis oris inferior (OOI) and mentalis (MTL). Electrode placements were based on anatomical landmarks from cadaveric studies (Kennedy and Abbs, 1979; Kahane and Folkins, 1984) and functional verification (Sussman et al., 1973). While anatomical localization of specific perioral muscles is problematic due to interdigitation of muscle fibers (Blair and Smith, 1986), verification procedures (e.g., the onset and offset of muscles consistent with their actions based on known orientation of muscle fibers, and the cessation of activity during antagonistic actions; see Smith et al., 1985) suggested that the muscles sampled were providing functionally specific electromyographic (EMG) information. Muscle activity was bandpass-filtered (50 Hz–2.5 kHz) and sampled at 2.5 kHz using a DEC PDP 11/44 lab

Received Aug. 6, 1987; revised Mar. 23, 1988; accepted May 11, 1988.

This work was supported by National Institute of Neurological and Communicative Disorders and Stroke Grants NS-20668, NS-13274 and NS-13617, and National Institute of Child Health and Human Development Grant HD-03352. The author thanks Kelly J. Cole for his comments on the manuscript and Deborah Hoffman for her excellent editorial assistance.

Correspondence should be addressed to Vincent L. Gracco, Ph.D., Haskins Laboratories, 270 Crown St., New Haven, CT 06511.

Copyright © 1988 Society for Neuroscience 0270-6474/88/124628-12\$02.00/0

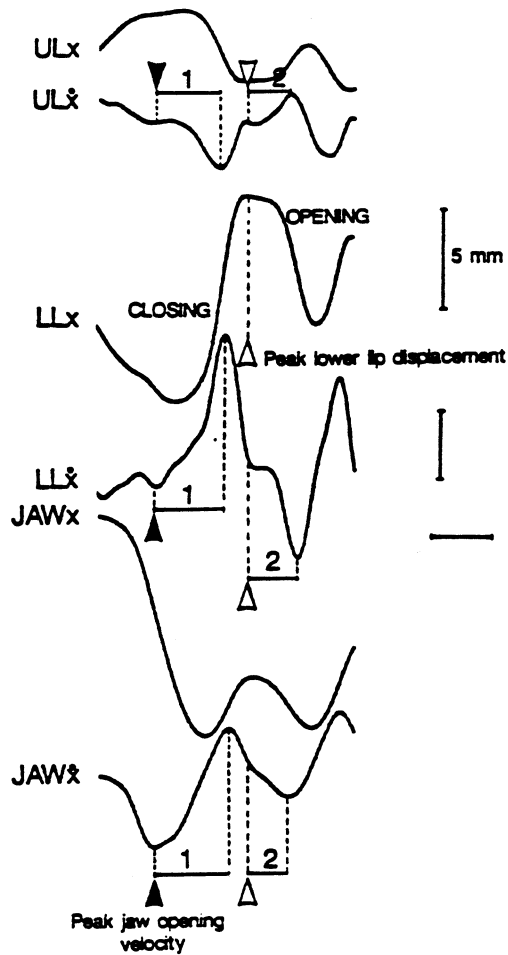


Figure 1. Schematic illustration of the timing analysis for the oral closing and subsequent oral opening movements associated with the first "p" and second "a" in "sapapple." As shown, all timing events for oral closing are referenced to the time of peak jaw opening velocity for the first "a" in "sapapple." The timing of the opening movements are relative to peak lower lip displacement for "p," generally reflecting oral closure. See text for further details; vertical calibrations for displacement (5 mm as marked), velocity (100 mm/sec), and time (100 msec).

computer (12-bit resolution). Inferior-superior movements of the upper lip, lower lip, and jaw were obtained using a head-mounted device described previously (Barlow et al., 1983). Briefly, a lightweight tubular frame was secured to the subject's head at the zygomatic and mastoid processes and the cranial vertex using rubber-tipped contact pads adjusted to eliminate head movement. The movement transducers were securely attached to the head-mounted frame and consisted of strain gages attached to cantilever beams oriented to capture inferior-superior movements of the lips and jaw. The rigid wire of the cantilever beams was inserted through a small piece of polyethylene tube coupled to the skin. The tubing was attached to the labial skin using a skin adhesive at the vermillion border and at a position on the chin that yielded negligible skin artifact (see Barlow et al., 1983; Kuehn et al., 1980, for discussion of placement yielding minimal artifact). Although some skin movement artifact may have been present, observations of independent action of the lip and jaw and observed movement differences (e.g., no jaw movement while the lower lip is elevating) suggest that any potential artifact was minimal. Movement signals were digitized at 500 Hz with no preacquisition filtering. Subjects were instructed to repeat the word "sapapple" at a preferred rate with even stress as if they were speaking to someone 15 feet away.

Data analysis. Following acquisition of approximately 70-150 repetitions per subject, the movement data were digitally low-pass-filtered

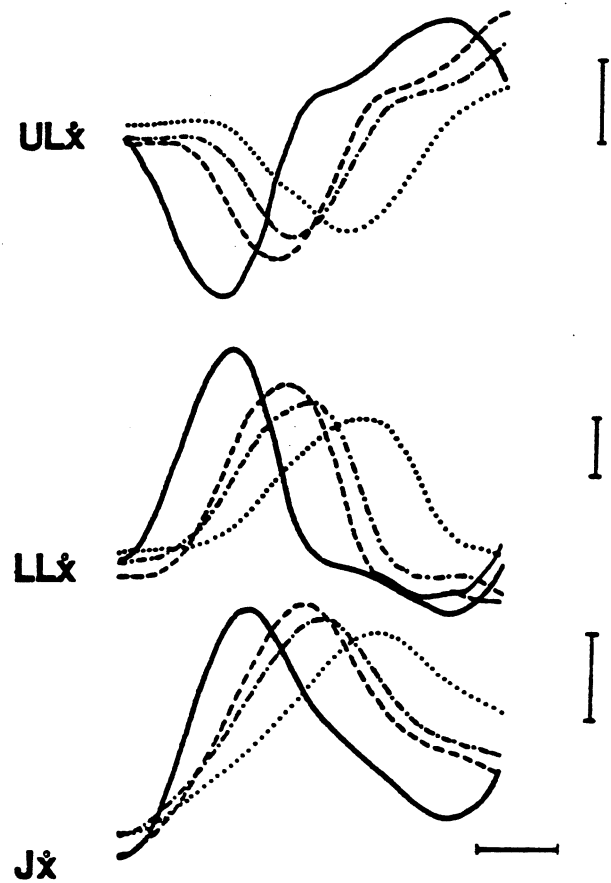


Figure 2. Four superimposed upper lip, lower lip, and jaw velocity profiles for the "p" closing movement illustrating the systematic adjustment in peak velocity timing for all structures with changes in movement speed. Calibration bars reflect 50 mm/sec (vertical) and 100 msec (horizontal).

(2-pole maximally flat; zero phase), and first derivatives were obtained using 3-point numerical differentiation (central difference). Prior to differentiation, the jaw signal was software-subtracted from the lower lip plus jaw signal, yielding net lower lip movement (see Gracco and Abbs, 1986). EMG signals were digitally rectified and low-pass-filtered (2-pole maximally flat; zero phase) at 20 Hz. From the filtered and derived signals, a number of temporal events were automatically identified with custom software algorithms; the events can be seen in Figure 1. Movement onset and offset were marked based on a 10% velocity criterion used in previous studies (Gracco and Abbs, 1986, 1988a). Briefly, movement onset was defined as the time when the velocity exceeded 10% of the peak for each particular movement. The use of a 10% criterion has been found to be useful in minimizing the identification of spurious onsets due to the elastic recoil of the tissue during continuous movements and identifying the active portion of movement initiation (accompanied by muscle action). Peaks in the velocity and EMG signals were identified, and all peak times were referenced to the time of peak jaw opening velocity preceding the closing movement. Peak jaw opening velocity was used since it provides an easily identifiable kinematic event prior to the movements of interest. EMG onsets, not shown in Figure 1, were software-identified from the low-pass-filtered signals and defined as the time when the background activity obtained a value 5% or greater than the peak value for the EMG activity associated with the particular closing movement. All identified EMG onsets were visually checked for appropriate placement. When excessive background activity was present, onsets were adjusted by visual identification, or if ambiguous, the trials were eliminated. For the subsequent opening movements, time of peak velocity was referenced to lower lip closure, defined as the time at which the velocity fell below 10% of the peak closing value (Fig. 1).

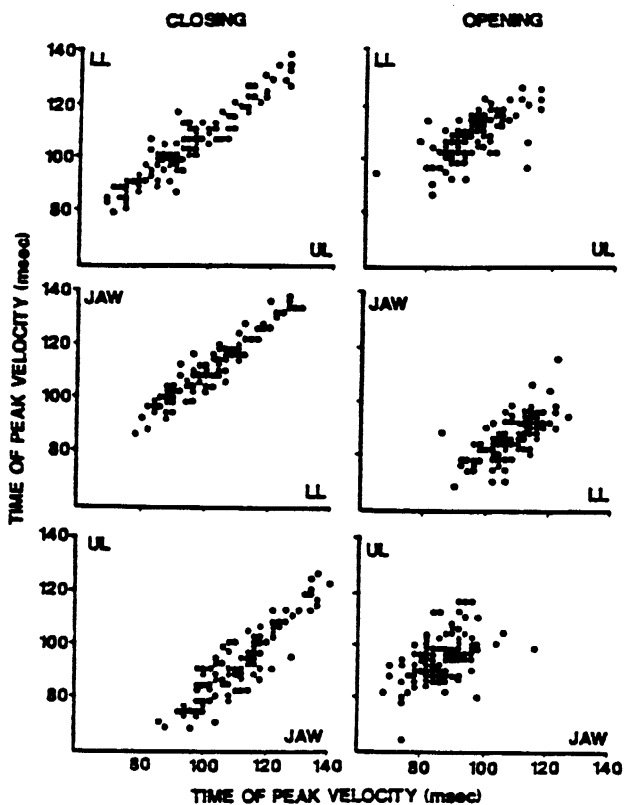


Figure 3. Scatterplots of the peak velocity timing relations among articulator pairs for closing and subsequent opening for upper lip, lower lip, and jaw movements for subject SM. The peak velocity timing relations for the opening movements are more variable than those for the closing movements. Further, the sequence of the velocity peaks are different for the opening and closing movements. For this subject, the sequence of occurrence for the closing movement is upper lip, lower lip, and jaw; for the opening movement, the jaw peak velocity occurred first, followed by the upper lip and lower lip. The peak velocity sequencing was found to be highly consistent across subjects for the closing movements and variable across subjects for the opening movements.

Results

Previous findings have demonstrated consistent timing and sequencing of upper lip, lower lip, and jaw peak velocities during oral closing (Gracco and Abbs, 1986, 1988a). The present study initially compared the timing and sequencing of labial opening movements to the labial closing movements.

Closing versus opening movements

A representative sample of the consistent sequencing of upper lip, lower lip, and jaw velocities for the first closing movement in "sapapple" is presented in Figure 2. As has been shown previously, the upper lip peak velocity occurs before the lower lip peak velocity, which occurs before the jaw peak velocity (Gracco and Abbs, 1986; Caruso et al., 1988) in a consistent manner with reversals (jaw before lower lip, or lower lip before upper lip) averaging less than 2% of the time. In the present study, of the total 502 responses from the 4 subjects, the upper lip/lower lip velocity sequence was reversed 3 times, and the lower lip/jaw velocity sequence was reversed 19 times. In contrast, the timing of opening peak velocities for the upper lip, lower lip, and jaw did not demonstrate the same consistency within or across subjects. As shown in Figure 3, the peak velocity

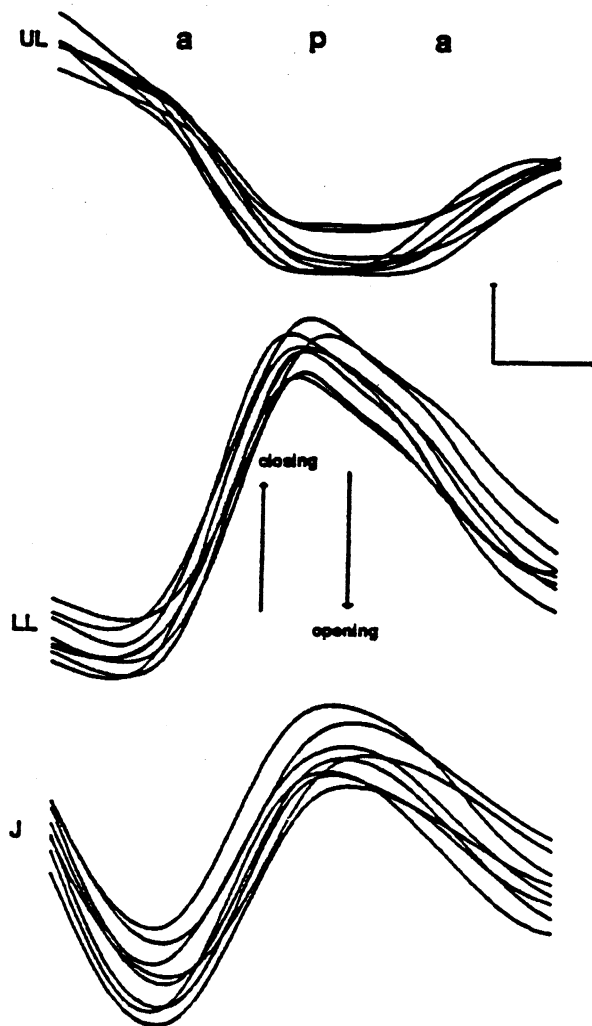


Figure 4. Superimposed upper lip, lower lip, and jaw movements for the first "p" closing and subsequent opening for the second "a" in "sapapple." For the "p" sound the lips approximate to allow the subsequent oral pressure build-up (the labial contact and compression are not seen due to the placement of the movement transducers on the vermillion border a few millimeters away from the contact area). As shown, the initial phase of the opening movement is accomplished by lower lip action, apparently reflecting the release of oral pressure associated with the "p" sound. Calibrations are 2 mm (vertical) and 50 msec (horizontal).

timing relations for closing and opening movements demonstrate that there are more variable opening peak velocity relations. Overall, peak opening velocities demonstrated a substantial number of reversals, ranging from 0 to 50%, and greater relational variability. To contrast the difference in the articulator timing relations for the opening and closing movements, linear regressions were obtained for all possible articulator pairs (Table 1). It can be seen from the slope comparisons and the coefficient of determination that the articulator timing relations are highly coupled for the closing movement and in many instances approach a unity slope. The opening movement velocity timing relations are apparently not tightly coupled and reflect more variable relations across and within subjects.

An additional difference in the upper lip, lower lip, and jaw peak velocity timing for closing versus opening movements is

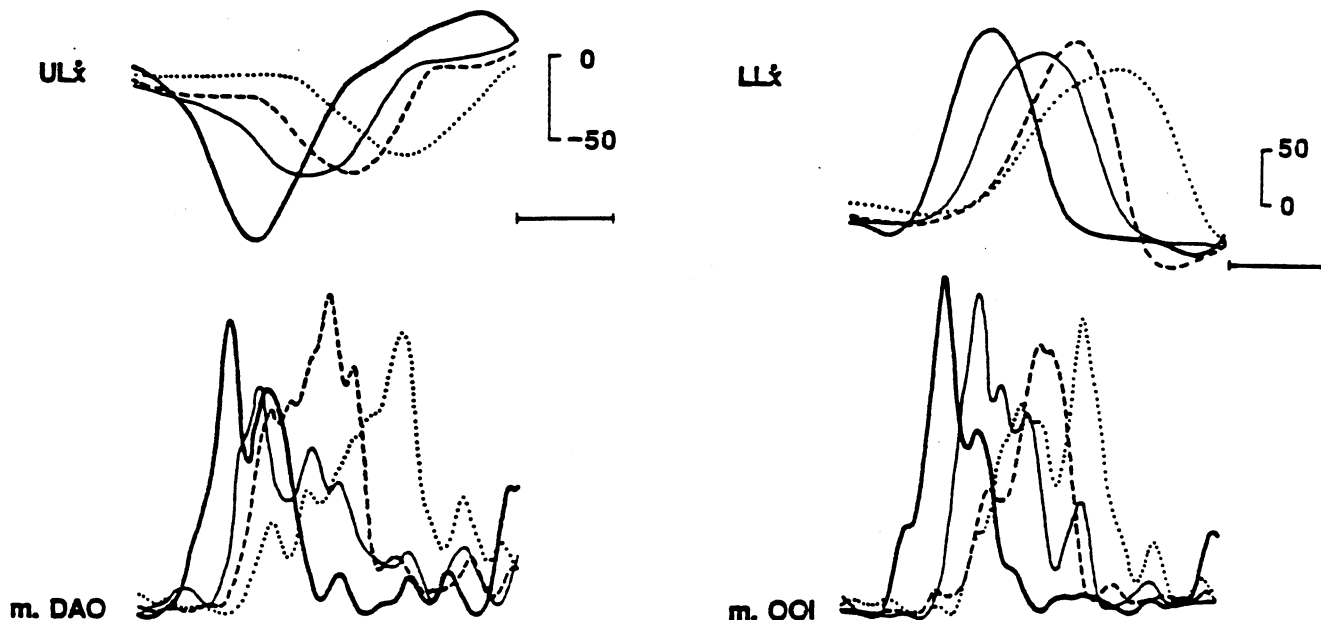


Figure 5. Four superimposed upper and lower lip movement velocity traces and the corresponding upper lip (*m. DAO*) and lower lip (*m. OOI*) muscle activity from subject DK. All traces are aligned to jaw opening peak velocity. Later-occurring muscle onsets are accompanied by later-occurring peak EMG amplitude and peak movement velocity timing for both the upper and lower lips. Vertical calibrations are in mm/sec, horizontal calibration is 50 msec.

in the order of their occurrence. Similar to previous studies (Gracco and Abbs, 1986, 1988a), all subjects in the present study demonstrated a sequential ordering of peak closing velocities (upper lip-lower lip-jaw); in contrast, the sequence of peak opening velocities was variable. For example, subjects demonstrated the following average sequence of opening peak velocity timing: upper lip-jaw-lower lip (2 subjects), lower lip-upper lip-jaw (1 subject), and jaw-lower lip-upper lip (1 subject). The only consistent pattern demonstrated for the opening movements is shown in Figure 4, in which the initial phase of opening always involved lower lip movement, while the upper lip and jaw maintained a quasi-postural or steady-state position. The early lower lip movement may reflect, in part, the release of the impounded intraoral air pressure associated with the "p" sound. Overall, it appears that the temporal characteristics of the opening and closing movements do not reflect a similar organization.

Muscle timing relations—closing movement

To examine the manner in which the underlying motor commands reflect speech movement coordination, the temporal characteristics of the multiple muscle patterns were examined.

Qualitatively, it was found that the timing of muscle onsets, peak EMG amplitudes, and peak movement velocities for oral closing all covaried. As illustrated in Figure 5, these temporal events were apparently adjusted in a systematic manner; later-occurring EMG onsets were accompanied by later-occurring EMG peak amplitudes that accompanied later-occurring peak movement velocities. However, in contrast to the consistent kinematic timing relations for oral closing, the muscle timing relations for the synergistic muscles associated with the closing movement were found to be more variable. For example, as shown in Figure 6, the ordering of muscle onsets reflects no consistent pattern across subjects. However, the timing of EMG onsets for individual subjects is apparently adjusted in a similar manner, as illustrated by the similarity of the onset relations in Figure 7. It appears that while the onset sequence is variable across subjects, the individual muscle onsets are generally adjusted in a consistent manner. The timing of peak EMG amplitude for all synergistic upper lip and lower lip muscles also reflected systematic relations. Shown in Figure 8 are the times of peak EMG amplitude for all possible combinations of the upper and lower lip muscles. Similar to EMG onsets, the general timing of peak EMG amplitudes from the multiple muscles

Table 1. Regression slope coefficients relating articulator pairs for the oral closing and following oral opening movements

Subject	Closing			Opening		
	UL-LL	UL-J	LL-J	UL-LL	UL-J	LL-J
CD (<i>n</i> = 148)	0.98 (0.93)	0.93 (0.93)	1.01 (0.97)	0.68 (0.17)	0.01 (0.01)	0.07 (0.01)
NV (<i>n</i> = 72)	0.87 (0.91)	0.79 (0.92)	0.90 (0.97)	1.04 (0.43)	0.86 (0.14)	0.76 (0.28)
SM (<i>n</i> = 119)	0.89 (0.88)	0.89 (0.86)	0.99 (0.94)	0.78 (0.45)	0.66 (0.32)	0.70 (0.48)
DK (<i>n</i> = 153)	0.98 (0.93)	1.04 (0.95)	1.04 (0.95)	1.30 (0.72)	0.58 (0.41)	0.46 (0.62)

Values in parentheses reflect the coefficient of determination (R^2) for the respective regressions.

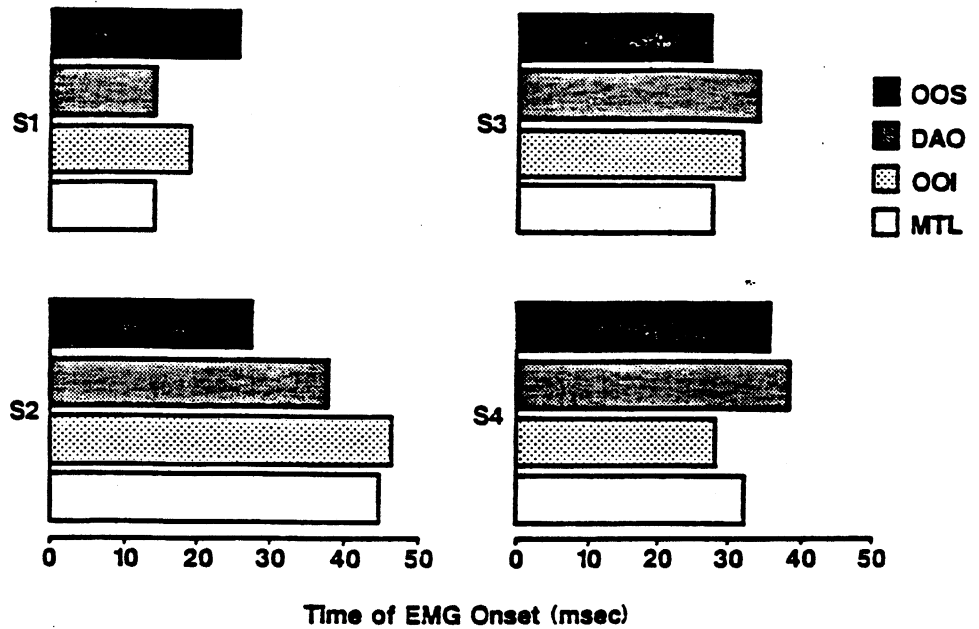


Figure 6. Summary of average EMG onsets of the 4 perioral muscles for the 4 subjects. Subjects are as follows: S1, subject CD; S2, subject NV; S3, subject SM; S4, subject DK. No across-subject consistency can be seen in the pattern of muscle onsets.

covary across multiple repetitions, although the slope relations across muscles are not as consistent as seen for the onset timing relations, possibly reflecting upper lip/lower lip differences.

EMG amplitude/peak velocity timing relations

In general, the EMG timing relations demonstrate that EMG onset and peak EMG amplitude timing covary in a systematic manner. In order to determine the degree to which these changes are related to the peak velocity timing relations, a linear model of EMG timing/peak velocity relations for the separate upper lip and lower lip was formalized and evaluated with a multiple regression procedure. A stepwise procedure was used with no

constraints on the order of entry into the procedure. It was also the case that specifying the order such that EMG onsets were entered before peak EMG amplitude timing resulted in exactly the same results. Figure 9 presents the predicted regression values versus the actual observed values for the data from subject CD. As can be seen, the linear model explains a substantial portion of the upper and lower lip closing velocity timing variation. Further, only one EMG onset coefficient reached statistical significance ($p < 0.05$) for each lip. Similar results were obtained for all subjects with R^2 values ranging from 66 to 94%. Of the possible 32 coefficients (4 subjects \times 4 independent variables \times 2 lips), only 6 were not significant ($p > 0.05$). Of the 6

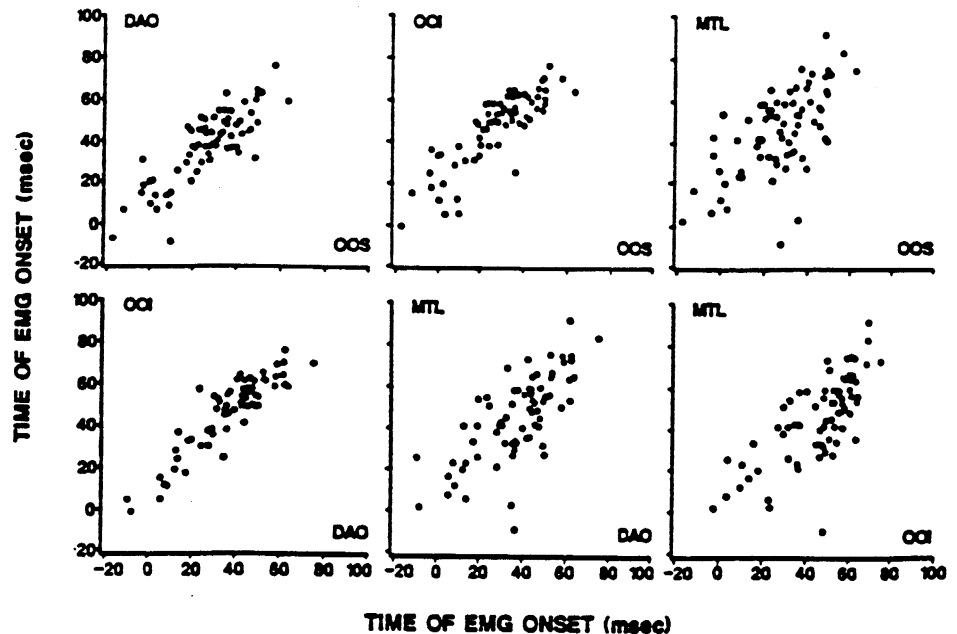


Figure 7. Data from subject NV illustrating the relations between EMG onset timing of different upper lip (DAO, OOS) and lower lip (OOI, MTL) muscles for multiple repetitions of the utterance "sapapple." All possible upper and lower lip combinations are presented. The timing of synergistic muscle onsets are seen to covary across multiple repetitions of "sapapple," illustrating the systematic relation of muscle onsets.

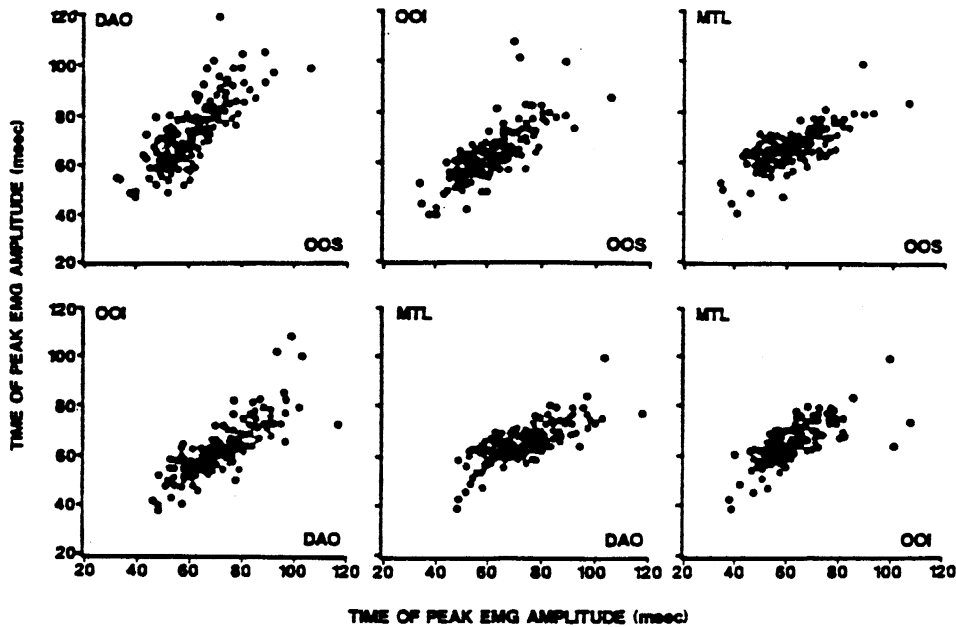


Figure 8. Data from subject SM illustrating the consistent peak amplitude timing relations among all upper and lower lip muscles. As shown, the timing of peak EMG amplitude is similarly adjusted for all synergistic muscles as movement duration changes.

nonsignificant coefficients, 5 were from muscle onset times, suggesting, as previously demonstrated, that the respective upper and lower lip muscle onsets are adjusted in a similar manner.

Upper lip-lower lip velocity timing differences

The present analysis has focused on similarities in the muscle activity patterns that produce the consistent timing relations for the upper and lower lip peak velocities, respectively. In considering the timing of the upper lip and lower lip movement velocities, a number of consistent differences were noted for all subjects. First, the time between upper lip muscle peak amplitude and upper lip peak velocity was shorter for all subjects compared with the same measure for the lower lip; average

values for each subject averaged across muscles were 12.05, 10.05, 13.5, and 7.7 msec for the upper lip and 23.7, 23.2, 27.7, and 13.4 msec for the lower lip for subjects CD, SM, DK, and NV, respectively; the lower lip difference was generally twice that of the upper lip. Second, as mentioned previously, the upper lip velocity peak occurred before the lower lip velocity peak for all subjects. The upper lip-lower lip peak velocity timing difference for the individual subjects averaged 7, 14, 16, and 16 msec for subjects CD, SM, DK, and NV, respectively. The observations that the time between peak EMG and peak velocity is greater for the lower lip relative to the upper lip, and the timing of the peak movement velocity is later suggests 2 possibilities. First, the upper and lower lips may have different

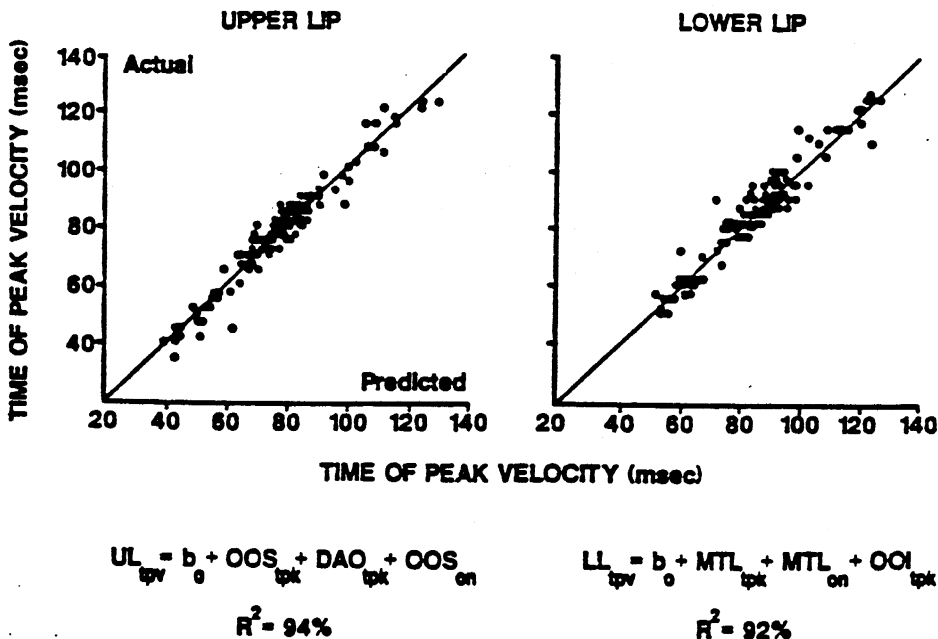


Figure 9. Results of multiple regression of EMG onset timing and time of peak EMG amplitude on upper and lower lip peak velocity timing. Shown are the results from subject CD and the general regression results for the upper and lower lips. One muscle onset time and both EMG peak times were included in the regression. The fitted line reflects unity slope; deviation from the line reflects any lack of fit.

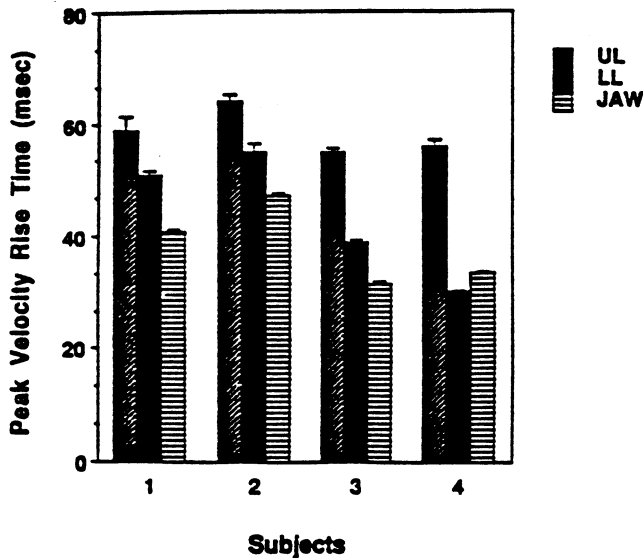


Figure 10. Velocity rise times for the upper lip, lower lip, and jaw for all subjects. Velocity rise times were obtained by calculating the time between the identified movement onset to the occurrence of peak velocity. The upper lip rise times were all longer than the lower lip rise times. For 3 of the 4 subjects the lower lip rise times were longer than the jaw rise times. The velocity rise time, reflecting the accelerative phase of the movement, indicates that the underlying forcing functions for the upper and lower lips are differentially adjusted, reflecting a planned temporally asynchronous action.

mechanical properties (inertia, stiffness), and providing coincidental forcing functions might result in the observed timing differences—a purely mechanical explanation. However, using a simple linear second-order kinematic model of the lips that included differential upper lip/lower lip stiffness (Ho et al., 1982), it was found that increasing the estimated mass by a factor of 4 and using the same force profile accounted for only about 4 msec of upper lip/lower lip peak velocity timing difference. It appears that the upper lip–lower lip velocity timing differences and the peak EMG–peak velocity timing differences for the upper and lower lips result in part from active neuromuscular adjustments.

In support of active neuromuscular changes contributing to the upper lip–lower lip timing differences are the data presented in Figure 10, which shows the velocity rise times of the upper lip, lower lip, and jaw for all subjects reflecting the accelerative phase of the individual movements. Because multiple muscles contribute to the observed movements and the muscle actions are generally asynchronous, it was felt that the rising portion of the movement velocity would provide a better indication of the underlying forcing function. As can be seen, the accelerative phase of the upper lip is much slower, as indicated by the longer rise time, than observed for the lower lip or jaw. This result suggests that a more gradual (lower frequency) forcing function is applied to the upper lip relative to the lower lip and jaw. As shown above, different mechanical properties of the upper and lower lips can account for only a portion of the upper lip–lower lip peak velocity timing differences. Rather, it appears that the underlying forcing functions for the upper and lower lips and jaw are adjusted in a manner to generate the asynchronous sequencing observed. Overall, the asynchronous timing of the upper lip, lower lip, and jaw movement is a planned component

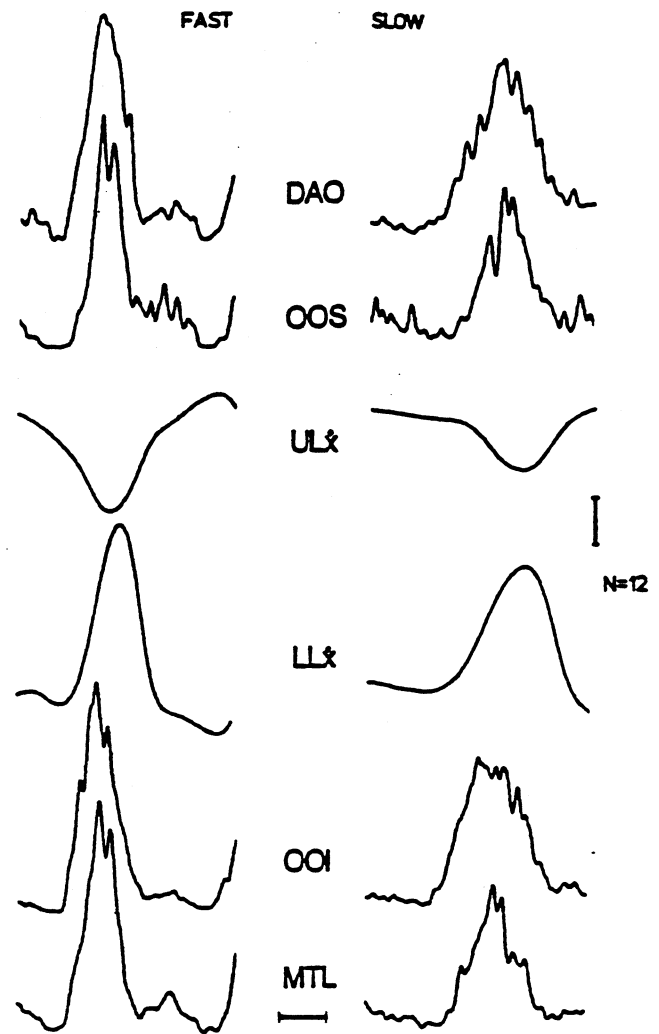


Figure 11. Averaged ($n = 12$) upper and lower lip muscle activity and resulting movement velocities for fast and slow production of “sapapple” (first “p” closing movement). Horizontal and vertical calibrations are 50 msec and 50 mm/sec, respectively; averages are aligned on peak jaw opening velocity. As shown, an increase in movement speed is accompanied by an increase in peak EMG amplitude, reduction in the EMG burst duration, and an earlier onset of muscle activity (re: jaw opening peak velocity).

of the coordination process resulting from multiple muscle timing and scaling adjustments.

Movement speed variations

As demonstrated by the above analysis, systematic changes in movement timing are accompanied by systematic changes in the time of onset and timing of peak EMG amplitude in all synergistic muscles. This can be seen clearly in Figure 11 in which one subject was instructed to produce “sapapple” at a fast (left) and a slow (right) rate of speech. For the fast movement, the average peak velocity and peak EMG amplitude were significantly greater compared with the slower movement ($p < 0.05$). Conversely, the maximum displacement, movement duration, integrated EMG area, and EMG rise time were all significantly reduced compared with the slower movement ($p < 0.05$). The systematic adjustment in EMG onset, the inverse

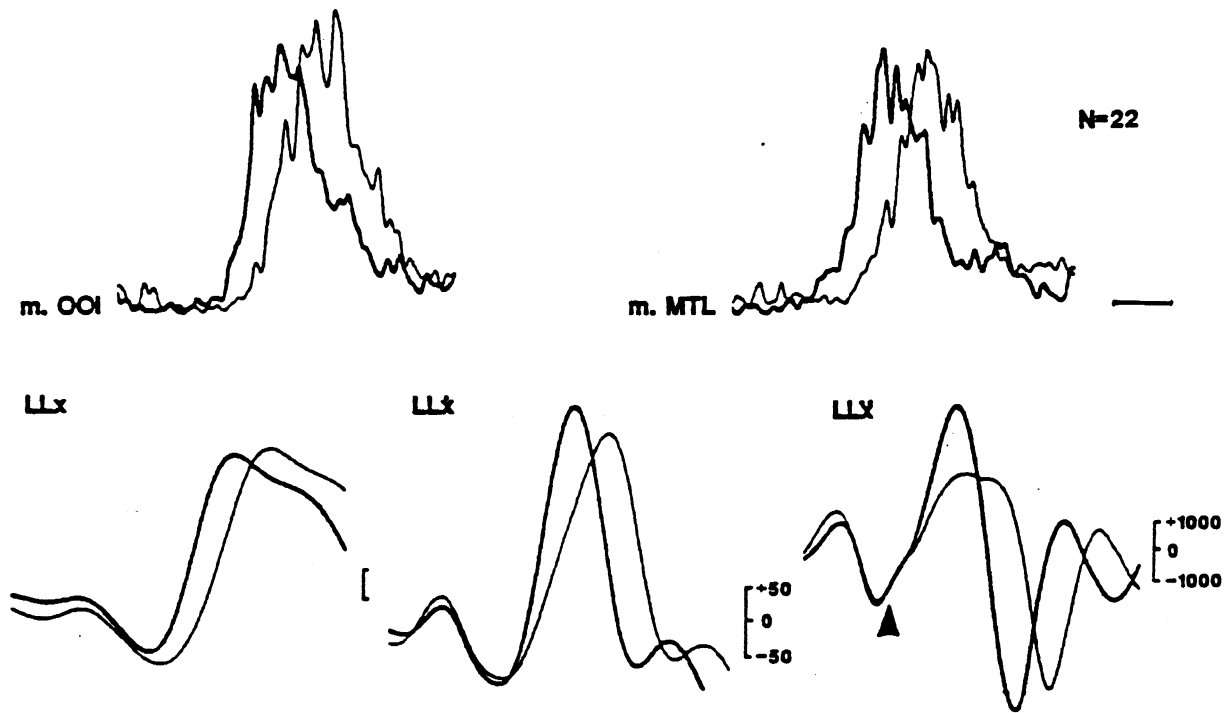


Figure 12. Averaged ($n = 22$) EMG activity and resulting lower lip movement displacement and movement acceleration for the first "p" closing movement in "sapapple"; darker lines indicate the faster movements. Grouping of movements were based on nonoverlapping distributions of relative peak velocity timing (range, 25 msec); averages were aligned on peak jaw opening velocity. Horizontal calibration is 50 msec, and vertical calibration for displacement is 1 mm; velocity and acceleration are in mm/sec and mm/sec². The faster movement is produced with EMG patterns similar to the slower movements with the exception of a slight time-advanced onset of muscle activity. The timing of the muscle onsets apparently allows the lip to achieve a higher and more phasic acceleration with no change in the magnitude of the muscle activity.

relation between EMG duration and peak EMG amplitude, and the resulting inverse relation between peak movement velocity and movement duration clearly reflect a temporal scaling of muscle activity patterns. However, these averages reflect large variations in movement timing. Examining small timing variations, on the order of 10–20%, it was found that changes in speaking rate can also be accomplished by modifications in the onset timing of muscle action alone (see also Gay, 1981). Presented in Figure 12 are averages of 22 lower lip movements of similar amplitude but different speed. As shown by the darker line, the faster movement was produced with similar (or smaller) peak EMG amplitudes. The major difference in the muscle activity is in the onset of the 2 lower lip muscles. The resultant effect of the earlier onset can be seen clearly in the kinematics. Prior to each movement, there is an apparent stretch and release of the labial tissue, which results in the rebound seen in the acceleration trace. The arrow reflects the onset of EMG for the faster movement, which coincides with the positive-going lower lip acceleration. The timing of the muscle action is adjusted to take maximum advantage of the elastic strain energy from the prestretch prior to the closing movement.

However, the apparent stretch of labial tissue prior to movement was not seen in all subjects. Other subjects demonstrated different patterns related to the utilization of the inherent mechanical properties of the lips and jaw. For example, for all subjects the initial acceleration for upper lip closing was observed prior to any observable muscle activation. The initial acceleration of the upper lip with no active muscle activation was hypothesized to result from the elastic recoil of the upper

lip following the labial stretch associated with the preceding opening movement. Similar observations were made for the lower lip and jaw. As shown in Figure 13, there is a significant initial acceleration in the jaw movement toward closure that is unaccompanied by an active muscle adjustment in the jaw closing muscle. It appears that the release of the antagonist coupled with the elastic recoil of the jaw following stretch provides a significant force to assist in the closing movement. Again, if the muscle onset was slightly earlier, it would be possible to attain a higher acceleration and a faster movement with no change in the magnitude of muscle activity. However, it should be noted that these observations are tentative due to the multiple muscles that can affect the lip and jaw movements and the difficulty in unambiguous electrode placement of the relevant muscles. The above observations are meant to be suggestive only and will require more careful and systematic evaluation. Overall, optimization of the mechanical energy store from the elastic properties of the lips and jaw was observed to varying degrees for all subjects.

Discussion

The present study evaluated the temporal characteristics of the multiple muscle actions and resulting movements associated with the coordination of the lips and jaw during speech. Coupled with recent findings demonstrating the maintenance of movement velocity timing relations following lip perturbation (Gracco and Abbs, 1988a), the present results provide further evidence for the central patterning of speech movements (Gracco and Abbs, 1986). The differential timing relations for move-

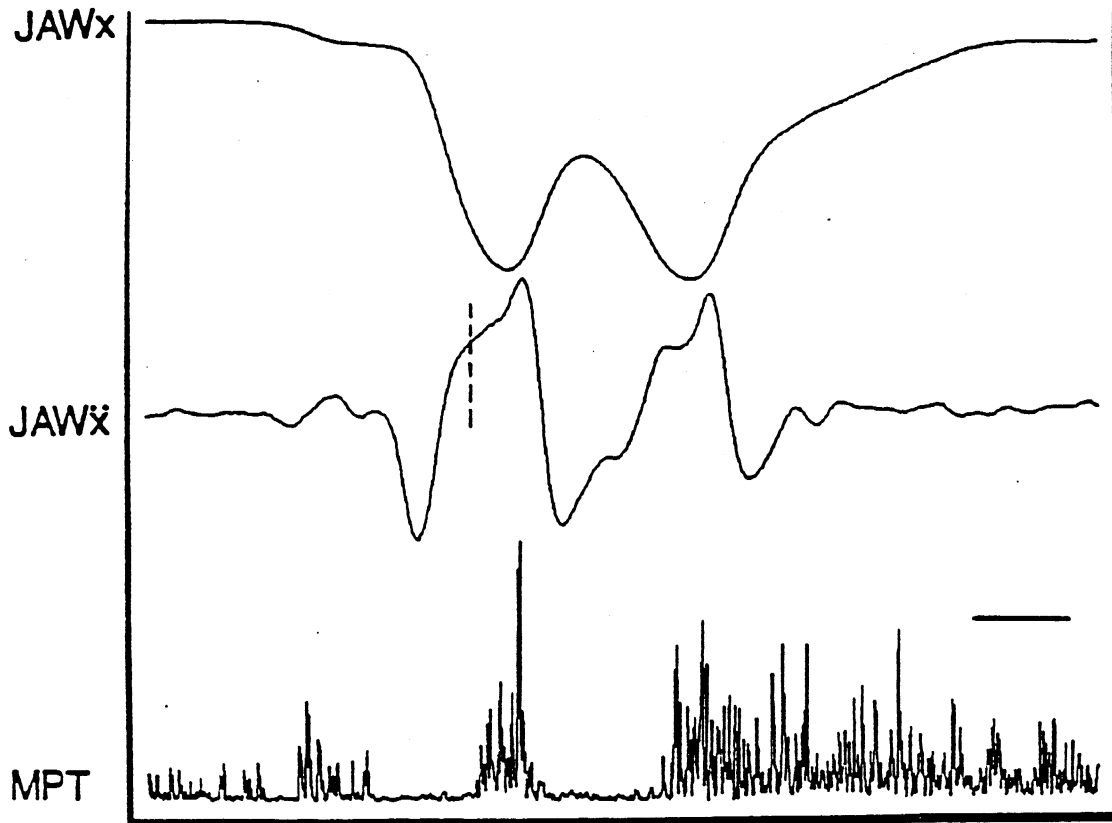


Figure 13. Single representative trial of the jaw opening and closing associated with the first "a" opening and the first "p" closing in "sapapple." Shown is the jaw displacement (x), jaw acceleration (\ddot{x}), and muscle activity from medial pterygoid (MPT), a jaw closer. The dotted line reflects the onset of the jaw closing muscle. From these observations it is tentatively concluded that the initial positive-going acceleration results from the combination of the release of the antagonist (not shown) coupled with the elastic rebound due to the stretch and release of the jaw closing muscles (primarily masseter).

ments in different directions (opening vs closing) appear to reflect the different task requirements and specific acoustic/aerodynamic consequences related to speech production. Further, these data suggest that the timing of central motor commands interacts with the mechanical properties of the speech articulators, minimizing energy expenditure and optimizing movement efficiency. The following discussion will expand on these areas, focusing on general principles underlying speech movement coordination.

Central patterning of speech movement timing

Similar to previous studies (Gracco and Abbs, 1986, 1988a; Caruso et al., 1988), the time course of the instantaneous velocities of the multiple lip and jaw movements reflects consistent and systematic timing adjustments characteristic of other patterned motor behaviors such as locomotion and chewing (Herman et al., 1976; Grillner, 1981; Luschi and Goldberg, 1981). For speech movement timing, the general tendency is for the timing of synergistic muscles active during oral closing to be adjusted in a similar manner. Similar to locomotion (Grillner and Zangger, 1975), muscle onsets were found to be highly related, although there was no consistent sequence of onsets across subjects. Previous EMG studies of jaw and lip muscles during speech have also reported inconsistent ordering of muscle onsets across subjects (Sussman et al., 1973; Folkins, 1981).

Given the small differences in onset timing and the consistent relationship between the respective muscle onsets, all synergistic muscles are apparently initiated by a common control signal. The subject-specific sequence of muscle onsets may result from a variety of factors, including electrode placement variation and/or small fluctuations in motoneuron pool excitability. Further, although movement/muscle timing can be influenced by phasic (perturbation) stimuli (Gracco and Abbs, 1988a), it appears that the onset of muscle activity is primarily a central phenomenon (see also Engberg and Lundberg, 1969; Grillner and Zangger, 1975, for locomotion). The systematic relations in the time course of all muscle patterns (e.g., onsets and time to peak amplitude) and the resulting kinematic relations are consistent with a temporal scaling of central motor commands to all synergistic muscles (e.g., "common drive"; DeLuca et al., 1982). As such, the nervous system uses the central patterning of muscle timing actions and the systematic modulation in the time course of synergistic motoneuron pools as a simplifying principle reducing the degrees of freedom to control. This is not to suggest that the individual muscles are performing the same redundant function; rather based on the different upper lip/lower lip muscle orientations, the synergistic muscles are more likely performing related but independent functions. The present results suggest that the temporal aspects of the multiple muscle actions are consistently and predictably related, and adjustments

in the timing of each individual muscle or structure (upper lip, lower lip, jaw) are organized to occur in a relationally consistent manner (see also Fowler, 1980; Tuller et al., 1982).

Characteristics of speech movement coordination

Speech movement coordination is apparently facilitated by relative timing relations among the multiple muscles and resulting movements. Such timing considerations among constituent components have been identified as a significant variable in the coordination of a variety of complex motor actions (Wadman et al., 1980; Lacquaniti and Soechting, 1982; Gracco and Abbs, 1986). The present study has demonstrated that for speech movements, the temporal characteristics of the EMG activity (onset, time to peak amplitude) are important variables in the coordination of the multiple articulators. The consistency of timing patterns is compatible with a coordinative strategy or a component of a "coordinative structure" (Fowler, 1977; Turvey, 1977) in which multiple components are functionally linked to reduce the degrees of freedom to control (Bernstein, 1967; Turvey et al., 1978). Although various forms of timing relations have been observed in other speech motor actions (Kent et al., 1974; Lofqvist and Yoshioka, 1981; Tuller et al., 1982; Harris et al., 1986) and for human locomotion (Herman et al., 1976), it is not clear whether consistent timing relations are characteristic of all multiarticulate motor behaviors or just specific to actions with significant temporal constraints due to multiple sequential adjustments. It is also interesting to note that although kinematic patterns across subjects were consistent, muscle activity patterns were seen to be more variable and subject specific. It may be that the intersubject variability reflects differences in labial and mandibular mechanical properties, electrode placement difficulties due to the interdigitation of labial muscle fibers (Blair, 1986; Blair and Smith, 1986), or merely the insensitivity of the kinematics to minor changes in muscle activity. Regardless, the consistent nature of the time course of the multiple muscle commands and their interaction provides the framework for the resulting multiarticulate coordination.

An interesting outcome from comparison of the opening and closing movement timing relations is the apparent modification in the specific coordination of the articulators with changing task requirements. For the closing movement, it is important that the upper lip, lower lip, and jaw are approximated within a restricted time interval for oral closing to allow the build-up of oral pressure. The highly related peak velocity timing across the lips and jaw apparently reflects the importance of the terminal phase of the movement for appropriately timed labial contact. In contrast, coordination of the lips and jaw for the opening movement is not critical in terms of final position or acoustic consequences. For the second "a" in "sapapple," the major acoustic consideration is the posterior constriction of the tongue within the oral cavity (Perkell and Nelson, 1982); the jaw opening movement has little effect on posterior tongue position (Kent and Moll, 1972). Rather, it is necessary that the opening actions of the upper lip, lower lip, and jaw be appropriately timed to produce the characteristic acoustic burst reflecting the release of oral pressure following closure; the consistently earlier onset of lower lip movement (Fig. 4) for the opening is consistent with this interpretation. It appears that the burst of acoustic energy characteristic of certain bilabial sounds ("p" and "b") results from the rapid lower lip opening movement following oral pressure build-up (Fig. 4). While it may be true that motor tasks with specific temporal require-

ments involve consistent timing relations, comparison of the opening and closing movement relations suggests that the form of such relations is variably specified. The closing/opening differences are also consistent with a recent study of sequential speech movements suggesting that each movement in a sequence can be differentially modified (Gracco and Abbs, 1988b). The capability of the speech motor system to adjust differentially each movement phase and the differential timing characteristics of the different movements suggest that opening movements and closing movements may reflect separate "synergies" (Bernstein, 1967), implicating each action as a basic component of speech production. Similarly, most human motor actions may involve the sequencing of a limited number of basic motor patterns, flexibly assembled for the task-specific goals. For speech production, the organizational characteristics of the constituent movements reflect the task-specific goals of the combined multi-movement actions included within a larger communicative framework (see also Saltzman, 1986).

Consideration of the consistent and apparently planned asynchronous upper lip-lower lip peak velocity sequencing allows for further speculation on the control of multiarticulate movements. In general, the upper lip movement reflects a phase-advanced action relative to the lower lip movement, resulting in the earlier occurrence of the upper lip peak velocity timing. The upper lip-lower lip ordering can be hypothesized to reflect a process in which the upper lip velocity provides time-advanced information to the lower lip or jaw regarding the timing and/or final position of the upper lip. More generally, the function of the timing offset in the lip and jaw velocity profiles may be to "feedforward" articulator information to adjust the positions or subsequent timing of upcoming sequential movements. This is consistent with previous speech motor control studies in which compensatory adjustments to perturbation are distributed to all functionally active structures (Folkins and Abbs, 1975; Abbs and Gracco, 1984; Kelso et al., 1984) in a manner dependent on the timing of the load relative to the unfolding motor action (Gracco and Abbs, 1985; Munhall and Kelso, 1985). Speech movement timing and hence the control of sequential speech motor actions appear to involve predictive adjustments to facilitate control speed and flexibility.

Neural-mechanical interactions

While the consistent kinematic and muscle timing relations reflect the planned coordination of the multiple structures, the biomechanical properties of the articulators are apparently used to facilitate the production of rhythmic speech movements. It was shown that non-neural factors such as elasticity can be used to facilitate the control and coordination of rhythmic speech movements. Consistent with this interpretation are results reported by Muller and MacLeod (1982) from cyclic loading experiments indicating that within the bandwidth of speech movements the passive tissue is primarily elastic in behavior. The elastic nature of the labial tissue suggests that the manner of the release due to antagonistic relaxation and the speed of the movement can result in different degrees of elastic rebound. It appears that appropriately adjusted neural signals can interact with the release of elastic strain energy to increase movement speed, strongly influencing the "efficiency" of rhythmic speech production. Further, the release of elastic strain energy, as was indicated for the lips and jaw, can be used to minimize the magnitude of activation required for certain speech movements. It is reasonable to suggest that the normal operational mode of

speech production exploits the biophysical properties of the speech structures through various active and passive adjustments. The maximization of such interaction defines the optimum efficiency state of neural-mechanical coupling of the speech structures. The suggestion that the preferred rate of speaking may be one that maximally exploits the energy supply components of the articulators and takes maximum advantage of these central-peripheral interactions also indicates that speaking faster or slower than the optimum may make increasing metabolic demands on the speech motor system (for broader discussion on preferred movement rates and adiabatic actions, see Kugler and Turvey, 1987). Specifically, rapid movements often produced with greater impedance effectively damp the elastic properties, while the timing of muscle action accompanying excessively slow movements may occur out of phase with the release. As such, speaking faster or slower than optimum may be achieved at a greater "cost" (Nelson, 1983). Additionally, inappropriately timed neural signals or a reduction in the range of movement as commonly accompanies movement disorders can minimize the ability to take advantage of the mechanical properties.

Investigations of the coordination of multiple-degrees-of-freedom systems have often resulted in the identification of simplifying relations among the components. For speech, as well as other rhythmic motor behaviors, the components are adjusted in terms of time and space. That is, the time course and magnitude of the individual actions must be adjusted to allow for their successful coordination. Representation and scaling of movement dynamics has been identified as potential simplifying strategies for both limb and speech movements (Hollerbach and Flash, 1982; Atkeson and Hollerbach, 1985; Saltzman, 1986; Saltzman and Kelso, 1987). However, the process of coordinating the multiple degrees of movement freedom is not inherent in the scaling of movement dynamics. The consistent timing relations identified in the present study reflect a simplification process in which all components are adjusted as a group rather than individually, effectively reducing the degrees of timing freedom to control (see Bernstein, 1967). As shown in the present study, the timing adjustments of the individual articulators involve systematic and predictable changes in multiple muscle onsets and peak amplitude timing. It appears that basic motor commands specifying relative onset, rise time, and duration for all relevant muscles are scaled according to task requirements. This constraint on the timing of individual muscle actions is one way in which the nervous system converts one important characteristic of the speech production process to a more controllable level.

References

- Abbs, J. H., and V. L. Gracco (1984) Control of complex motor gestures: Orofacial muscle responses to load perturbations of the lip during speech. *J. Neurophysiol.* 51: 705-723.
- Atkeson, C. G., and J. M. Hollerbach (1985) Kinematic features of unrestrained vertical arm movements. *J. Neurosci.* 5: 2318-2330.
- Barlow, S. M., K. J. Cole, and J. H. Abbs (1983) A new head-mounted lip-jaw movement transduction system for the study of motor speech disorders. *J. Speech Hear. Res.* 26: 283-288.
- Bernstein, N. (1967) *The Co-ordination and Regulation of Movements*. Pergamon, New York.
- Blair, C. (1986) Interdigitating muscle fibers throughout orbicularis oris inferior: Preliminary observations. *J. Speech Hear. Res.* 29: 266-269.
- Blair, C., and A. Smith (1986) EMG recording in human lip muscles: Can single muscles be isolated? *J. Speech Hear. Res.* 29: 256-266.
- Caruso, A. J., J. H. Abbs, and V. L. Gracco (1988) Kinematic analysis of speech multiple movement coordination in stutterers. *Brain* 111: 439-456.
- DeLuca, C. J., R. S. LeFever, M. P. McCue, and A. P. Xenakis (1982) Control scheme governing concurrently active human motor units during voluntary movements. *J. Physiol. (Lond.)* 329: 129-142.
- Engberg, I., and A. Lundberg (1969) An electromyographic analysis of muscular activity in the hind limb of the cat during unrestrained locomotion. *Acta Physiol. Scand.* 75: 614-630.
- Folkins, J. W. (1981) Muscle activity for jaw closing during speech. *J. Speech Hear. Res.* 24: 601-615.
- Folkins, J. W., and J. H. Abbs (1975) Lip and jaw motor control during speech: Responses to resistive loading of the jaw. *J. Speech Hear. Res.* 18: 207-220.
- Fowler, C. A. (1977) *Timing Control in Speech Production*. Indiana University Linguistics Club, Bloomington.
- Fowler, C. A. (1980) Coarticulation and theories of extrinsic timing. *J. Phonetics* 8: 113-133.
- Gay, T. (1981) Mechanisms in the control of speech rate. *Phonetica* 38: 148-158.
- Gel'fand, I. M., V. S. Gurfinkel, M. L. Tsetlin, and M. L. Shik (1971) Some problems in the analysis of movements. In *Models of the Structural-functional Organization of Certain Biological Systems*. I. M. Gel'fand, V. S. Gurfinkel, S. V. Fromin, and M. L. Tsetlin, eds., MIT Press, Cambridge, MA.
- Gracco, V. L., and J. H. Abbs (1985) Dynamic control of perioral system during speech: Kinematic analyses of autogenic and nonautogenic sensorimotor processes. *J. Neurophysiol.* 54: 418-432.
- Gracco, V. L., and J. H. Abbs (1986) Variant and invariant characteristics of speech movement planning. *Exp. Brain Res.* 65: 156-166.
- Gracco, V. L., and J. H. Abbs (1988a) Central patterning of speech movement timing. *Exp. Brain Res.* 71: 515-526.
- Gracco, V. L., and J. H. Abbs (1988b) Sensorimotor characteristics of speech movement sequences. *Exp. Brain Res.* (in press).
- Grillner, S. (1975) Locomotion in vertebrates: Central mechanisms and reflex interaction. *Physiol. Rev.* 55: 247-304.
- Grillner, S. (1981) Control of locomotion in bipeds, tetrapods, and fish. In *Handbook of Physiology: Section 1. The Nervous System: Vol. 2. Motor Control*, Pt. 1, V. B. Brooks, ed., pp. 1179-1236, American Physiological Society, Bethesda, MD.
- Grillner, S., and P. Zangger (1975) How detailed is the central pattern generation for locomotion? *Brain Res.* 88: 367-371.
- Harris, K. S., B. Tuller, and J. A. S. Kelso (1986) Temporal invariance in the production of speech. In *Invariance and Variability in Speech Processes*. J. S. Perkell and D. H. Klatt, eds., pp. 243-252, Erlbaum, Hillsdale, NJ.
- Herman, R., R. Wirta, S. Bampton, and F. R. Finley (1976) Human solutions for locomotion: Single limb analysis. In *Neural Control of Locomotion*. R. M. Herman, S. Grillner, P. S. G. Stein, and D. G. Stuart, eds., pp. 13-49, Plenum, New York.
- Ho, T. P., K. Azar, S. Weinstein, and W. W. Bowley (1982) Physical properties of human lips: Experimental and theoretical analysis. *J. Biomech.* 15: 859-866.
- Hollerbach, J. M., and T. Flash (1982) Dynamic interactions between limb segments during planar arm movement. *Biol. Cybernet.* 44: 67-77.
- Kahane, J. C., and J. F. Folkins (1984) *Atlas of Speech and Hearing Anatomy*. Charles E. Merrill, Columbus, OH.
- Kelso, J. A. S., B. Tuller, E. V. Bateson, and C. A. Fowler (1984) Functionally specific articulatory cooperation following jaw perturbations during speech: Evidence for coordinative structures. *J. Exp. Psychol. [Hum. Percept.]* 10: 812-832.
- Kennedy, J. G., and J. H. Abbs (1979) Anatomic studies of the perioral motor system: Foundations for studies in speech physiology. In *Speech and Language: Advances in Basic Research and Practice*, Vol. 1, N. J. Lass, J. L. Northern, D. E. Yoder, L. V. McReynolds, eds., pp. 211-270, Academic, New York.
- Kent, R. D., and K. L. Moll (1972) Cinefluorographic analysis of selected lingual consonants. *J. Speech Hear. Res.* 15: 453-473.
- Kent, R. D., and R. Netsell (1971) Effects of stress contrasts on certain articulatory parameters. *Phonetica* 24: 23-44.
- Kent, R. D., P. J. Carney, and L. R. Severid (1974) Velar movement and timing: Evaluation of a model for binary control. *J. Speech Hear. Res.* 17: 470-488.
- Kent, R. D., and K. L. Moll (1975) Articulatory timing in selected consonant sequences. *Br. Lang.* 2: 304-323.

- Kuehn, D. P., A. R. Reich, and J. E. Jordan (1980) A cineradiographic study of chin marker positioning: Implications for the strain gauge transduction of jaw movement. *J. Acoust. Soc. Am.* 67: 1825-1827.
- Kugler, P. N., and M. T. Turvey (1987) *Information, Natural Law, and the Self-assembly of Rhythmic Movement*. Erlbaum, Hillsdale, NJ.
- Lacquaniti, F., and J. F. Soechting (1982) Coordination of arm and wrist motion during a reaching task. *J. Neurosci.* 2: 399-408.
- Lofqvist, A., and H. Yoshioka (1981) Interarticulator programming in obstruent production. *Phonetica* 38: 21-34.
- Luschei, E. S., and L. J. Goldberg (1981) Neural mechanisms of mandibular control: Mastication and voluntary biting. In *Handbook of Physiology. The Nervous System*, Vol. 2, Chap. 27, pp. 1237-1274, V. B. Brooks, ed., American Physiological Society, Bethesda, MD.
- Muller, E. M., and G. M. MacLeod (1982) Perioral biomechanics and its relation to labial control. *J. Acoust. Soc. Am.* 71: S33.
- Munhall, K. G. (1985) An examination of intra-articulator relative timing. *J. Acoust. Soc. Am.* 78: 1548-1553.
- Munhall, K. G., and J. A. S. Kelso (1985) Phase-dependent sensitivity to perturbation reveals the nature of speech coordinative structures. *J. Acoust. Soc. Am.* 78: S38.
- Nashner, L. M. (1977) Fixed patterns of rapid postural responses among leg muscles during stance. *Exp. Brain Res.* 30: 13-24.
- Nelson, W. L. (1983) Physical principles for economies of skilled movements. *Biol. Cybernet.* 46: 135-147.
- Perkell, J. S., and W. L. Nelson (1982) Articulatory targets and speech motor control: A study of vowel production. In *Speech Motor Control*, S. Grillner, B. Lindblom, J. Lubker, and A. Persson, eds., pp. 187-204. Pergamon, Oxford.
- Saltzman, E. (1986) Task dynamic coordination of the speech articulators: A preliminary model. In *Generation and Modulation of Action Patterns*. H. Heuer and C. Fromm, eds., pp. 129-144. Springer-Verlag, Berlin.
- Saltzman, E., and J. A. S. Kelso (1987) Skilled actions: A task-dynamic approach. *Psychol. Rev.* 94: 84-106.
- Shik, M. L., and G. N. Orlovsky (1976) Neurophysiology of locomotor automatism. *Physiol. Rev.* 56: 465-501.
- Smith, A., C. A. Moore, D. H. McFarland, and C. M. Weber (1985) Reflex responses of human lip muscles to mechanical stimulation during speech. *J. Motor Behav.* 17: 131-147.
- Soechting, J. F., and F. Lacquaniti (1981) Invariant characteristics of a pointing movement in man. *J. Neurosci.* 1: 710-720.
- Sussman, H. M., P. F. MacNeilage, and R. J. Hanson (1973) Labial and mandibular dynamics during the production of bilabial consonants: Preliminary observations. *J. Speech Hear. Res.* 16: 397-420.
- Tuller, B., and J. A. S. Kelso (1984) The timing of articulatory gestures: Evidence for relational invariants. *J. Acoust. Soc. Am.* 76: 1030-1036.
- Tuller, B., J. A. S. Kelso, and K. S. Harris (1982) Interarticulator phasing as an index of temporal regularity in speech. *J. Exp. Psychol.* 8: 460-472.
- Turvey, M. T. (1977) Preliminaries to a theory of action with reference to vision. In *Perceiving, Acting and Knowing: Towards an Ecological Psychology*, R. Shaw and J. Bransford, eds., Erlbaum, Hillsdale, NJ.
- Turvey, M. T., R. Shaw, and W. Mace (1978) Issues in the theory of action: Degrees of freedom, coordinative structures and coalitions. In *Attention and Performance*, Vol. 7, J. Requin, ed., Erlbaum, Hillsdale, NJ.
- Wadman, W. J., J. J. Denier van der Gon, and R. J. A. Derksen (1980) Muscle activation patterns for fast goal-directed arm movements. *J. Hum. Movement Stud.* 6: 19-37.