

Central patterning of speech movements

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Summary. Previous speech kinematic studies have demonstrated systematic timing relations among the upper lip, lower lip, and jaw suggesting the operation of a central pattern generator (CPG). The present study evaluated the consistency of these timing relations following unanticipated perturbation of the lower lip. Using this approach, it was also possible to evaluate the influence of sensory information on the timing of motor output and subsequent coordination of the multiple speech movements. Perturbations were applied to the lower lip during the closing movement associated with the first “p” in “sapapple”. Muscle activity and movements of the upper lip, lower lip, and jaw were obtained. Changes in movement displacement, velocity and duration, the timing and sequencing of peak velocities, EMG area, and EMG rise time were analyzed for the control and load conditions. Similar to previous perturbation results, significant magnitude compensations from the muscles and movements of the upper lip, lower lip, and jaw were observed. In contrast, movement durations and the sequencing of peak velocities were relatively unaffected by the lower lip load. The timing of peak EMG amplitude and consequently the timing of peak closing velocity for all structures (UL, LL, and J) occurred earlier relative to the preceding opening movement. These results are consistent with the interaction of phasic sensory input with centrally-driven commands resulting in a phase-advanced motor output. Further, as the timing of one structure is modified so were all the functionally-linked components thereby maintaining the necessary coordination. As in other rhythmic motor behaviors such as locomotion and chewing, there appears to be a centrally patterned framework for speech movement coordination.

Key words: Coordination – Timing – Speech movements – Central patterning – Sensorimotor

Introduction

A hallmark of most multiarticulate motor behaviors is the coordinated action of multiple structures. Such diverse actions as walking, insect flight, swimming, mastication, and speech rely extensively on multimovement interactions. The more automatic of these behaviors (e.g., insect flight, swimming, mastication, and locomotion) have been shown to rely on central generators which produce patterned motor output (Chandler and Goldberg 1984; Dellow and Lund 1971; Eidelberg et al. 1981; Getting 1981; Grillner and Wallen 1984, 1985; Lennard and Hermanson 1985; Lund and Dellow 1969; Wilson 1961). However, flight, mastication, and treadmill locomotion are essentially continuous rhythmical actions ideally suited for modulated stereotypic synaptic interactions. Speech movements, while rhythmical, are more appropriately considered episodic, requiring more variable adjustments. The extent to which pattern generator-like processes and hence common neuronal mechanisms underlie more variable, less automatic motor behaviors such as speech is unknown.

Previously, it was suggested that a central pattern generator or pattern-generator-like process was responsible for the consistency of speech movement timing (Gracco and Abbs 1986). Specifically, the movement onsets and times of peak velocity for the upper lip (UL), lower lip (LL), and jaw (J) were found to be sequentially ordered and proportionally adjusted with changes in movement speed (Gracco and Abbs 1986). These timing relations have been shown to be associated with adjustments in the time

course of muscle activation patterns for the synergistic muscles of the lips and jaw (Gracco 1986). However, from previous studies, it is not clear whether the timing relations observed reflect a planned component of speech movement coordination or merely reflect an artifact due to the experimental consistency required to minimize variations in speaking stress and rate. One means to test the significance of the relative timing relations is to perturb one of the multiple speech movements and examine the resulting temporal adjustments. If movement timing relations are not maintained following perturbation, it can be concluded that such timing relations are not an important control parameter for speech movement coordination. However, if certain timing relations are maintained in the compensatory adjustments, it can be assumed that the timing among the multiple structures is an essential characteristic of the underlying coordination process. The present results suggest that consistent timing relations among the multiple movements reflect a significant property of the speech motor control system apparently relying on central patterning to facilitate coordination. Further, sensory influences are incorporated within the central patterning of these timing relations allowing for interactive multiarticulate adjustments.

Material and methods

Subjects – Four adult subjects (3 females, 1 male) between the ages of 23 to 29 were used in the present study. All were naive to the purpose of the experiment and none had previously participated in motor control investigations.

Movement Task – Subjects repeated the utterance “sapapple” following the presentation of a tone; the tone was used as a cue to begin. Each trial was initiated with the subject at rest, lips and teeth lightly touching. There were no specific requirements imposed on the subjects; the only instructions were to speak at a moderate vocal intensity that was understandable 10 to 15 feet away. Intertrial interval was approximately 5 s. Inferior-superior movements of the upper lip, lower lip, and jaw were transduced using ultra-light weight cantilever beams instrumented with strain gauges attached to a lightweight head-mounted frame (Barlow et al. 1983). Transducers were attached midsagittally at the vermilion border of the upper and lower lips; the jaw transducer was placed under the chin in a location that yielded negligible artifact from skin movement.

On approximately 15% of the trials, a 45-g force (15 ms rise time) was applied to the lower lip prior to the onset of muscle activity associated with the first “p” closure. Perturbations were delivered to the lower lip using a torque motor operating under force feedback control (cf. Abbs and Gracco 1984 for details). The load remained on for the duration of the closing movement.

Muscle activity

Electromyographic (EMG) activity was recorded from two upper lip depressor muscles (Orbicularis oris superior-OOS and De-

pressor anguli oris-DAO) and two lower lip elevator muscles (Orbicularis oris inferior-OOI and Mentalis-MTL) using hooked-wire electrodes. EMG activity was obtained through 70 micron copper wire deinsulated at the tip (1 mm) and spaced approximately 4 mm apart per muscle. In one subject, EMG activity was obtained from Medial pterygoid (MPT), a jaw closing muscle instead of MTL. EMG signals were bandpass filtered (50 to 2500 Hz) and amplified prior to data acquisition.

Data acquisition – All signals were digitized on-line using a PDP 11/44 lab computer (12 bit resolution). Movement signals were digitized at 500 sps; EMG signals were digitized at 2500 sps. Prior to kinematic analysis, all movement signals were digitally filtered (20 Hz lowpass) using a two-pole Butterworth design in the forward and backward direction to eliminate phase distortion. First derivatives were obtained by a three-point numerical differentiation of the filtered movement signals. Similarly, EMG signals were digitally rectified and lowpass filtered at 100 Hz using a two-pole Butterworth design in the forward and backward direction.

Data analysis – All kinematic and electromyographic analysis focused on the first “p” closing movement in “sapapple”. Prior to the determination of relevant kinematic events, the lower lip signal, which reflects the combined contribution of the lower lip and jaw, was software subtracted from the lower lip plus jaw signal, yielding net lower lip movement. Movement onset was then identified from the instantaneous velocity profile during the closing movement and defined as the point at which movement velocity achieved 10% of the peak velocity for the individual movement. Movement offset was defined as the point at which the peak velocity fell below 10% of the peak velocity for each individual movement. While a 10% velocity criterion is somewhat conservative it was found to be necessary due to the elastic properties of the labial tissue and the continuous nature of the movements under investigation. Using a 1% or even 5% criterion often resulted in the identification of onsets prior to muscle activity. Further, in a previous study (Gracco and Abbs 1986) the use of 1% or 5% velocity criterion did not change the results in any appreciable manner. All movement onsets and offsets were identified using a computer algorithm. Closing displacement and movement duration were defined as the distance and time between movement onset and movement offset, respectively. The onset of muscle activity was identified visually using both the raw unprocessed and processed EMG signals. In order to minimize EMG onset bias, the activity of each muscle was viewed independently and the onset identified without concomitant viewing of the activity of other muscles.

Based on the identified time points, kinematic measures were obtained for peak movement displacement, peak instantaneous velocity, movement duration, and the time of peak velocity (relative to jaw opening peak velocity). EMG measures included integrated area for a 100 to 120 ms interval from EMG onset, peak EMG amplitude, time of EMG onset, and time of peak EMG; (all temporal measures were made relative to jaw opening peak velocity). A summary of the analysis procedures are presented in Fig. 1.

Results

As in the previous study (Gracco and Abbs 1986) the peak velocities were consistently ordered in time (viz., UL, LL, J) and varied proportionally with movement duration. The present investigation focused on the consistency of the timing measures following disruptive changes requiring compensatory movement adjustments. In order to facilitate the

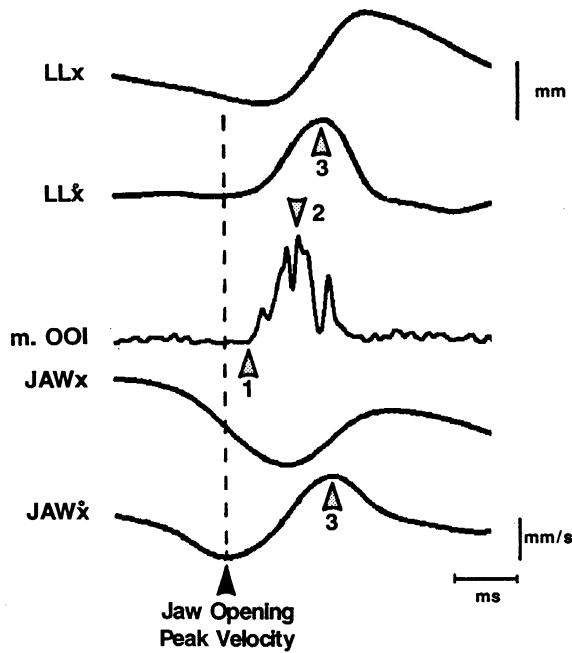


Fig. 1. Illustration of events used in the load/control analysis (see text for details). Arrows identify the variables of interest in the present study. Arrow 1: EMG onset; arrow 2: time and magnitude of peak EMG amplitude; arrow 3: time and magnitude of peak movement velocity. All timing measures were referenced to the occurrence of jaw opening peak velocity for the first "a" in "sapapple". Measurements were made on the closing movement for the first "p" in 'sapapple'. Vertical calibration are 2 mm and 50 mm/s, horizontal calibration is 50 ms

interpretation of the timing results, compensatory movement displacement, velocity, and durational changes were first examined. Overall, it appeared that the compensatory adjustments for all subjects were integrated into the patterned motor output with modifications distributed among the multiple movements.

Movement compensation

Consistent with an earlier study of labial responses to LL perturbation (Gracco and Abbs 1985), UL and LL movement displacement increased with the LL load. In addition, perturbation of LL movement prior to oral closure resulted in increased displacement of the J for all subjects. The significant increase in relative J displacement is of interest; previously J movement changes to LL perturbation had only been observed following electrical stimulation of the LL depressor muscle (Folkens and Zimmermann 1982). Hence, the present finding indicates that LL afferents, responding to stretch and pressure, can access and modify J muscle actions. Based on the lack of

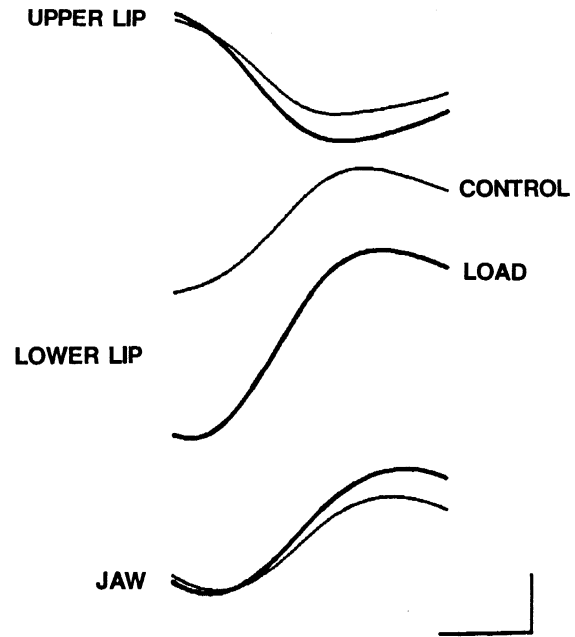


Fig. 2. Averaged upper lip (UL), lower lip (LL), and jaw (J) closing movements for the control (thin line) and load (thick line) conditions ($n = 72$ for both conditions). Vertical calibration is 2 mm, horizontal calibration is 50 ms

any perceptible speech delays following introduction of the perturbation it can be assumed that compensatory J muscle actions occurred within the latency range previously reported for lip muscles following labial perturbation (Abbs and Gracco 1984). Figure 2 illustrates the average increase in the extent of UL, LL, and J displacement to the load for subject 1. A summary of the UL, LL, and J displacement and velocity changes for all subjects is presented in Table 1. As indicated, all subjects demonstrated statistically significant increases in UL, LL, and J peak displacement to the load ($p < 0.05$, t-test for paired data). The peak velocity changes were somewhat more variable; however, increasing movement velocity with load can be seen for all subjects.

In contrast to the consistent movement displacement changes, movement duration changes were less consistent. As seen qualitatively in Fig. 2, although the compensatory closing movements were significantly increased in relative displacement, the load and control movement durations are quite similar. Figure 3 summarizes the movement duration changes for all subjects expressed as a percent change (re: control). As shown, UL, LL, and J movement durations changed minimally, rarely increasing by more than 12%; average absolute load/control differences in movement duration for all subjects ranged from -2 to 14 ms.

Table 1. Summary of the average UL, LL, and J movement displacement (mm) and velocity (mm/s) for the control (C) and load (L) conditions. Numbers in parentheses reflect one standard deviation. All C-L-comparisons are significantly different at $p < 0.05$ except where indicated (*)

	Displacement						Velocity					
	UL		LL		J		UL		LL		J	
S1	4.3 (0.8)	5.3 (0.9)	4.7 (1.3)	7.3 (2.0)	3.4 (1.1)	4.5 (1.1)	79.2 (12.7)	95.1 (15.8)	96.3 (26.1)	131.4 (41.2)	68.0 (18.7)	80.5 (18.1)
S2	5.9 (0.9)	6.4 (1.0)	4.5 (1.1)	7.8 (1.7)	4.0 (1.0)	5.2 (1.1)	139.9 (33.4)	141.3* (38.7)	141.9 (20.6)	170.2 (21.8)	104.7 (14.6)	117.9 (16.2)
S3	6.5 (0.9)	7.7 (0.9)	3.9 (0.6)	4.4 (0.9)	4.4 (0.9)	4.8 (0.9)	95.4 (11.2)	101.7 (10.5)	84.5 (12.2)	84.0* (15.0)	82.0 (15.8)	85.4 (13.6)
S4	4.4 (0.6)	4.8 (0.7)	9.8 (1.4)	12.0 (2.0)	4.2 (0.9)	4.7 (1.1)	75.3 (11.4)	77.3* (12.1)	198.2 (31.7)	204.3* (44.0)	83.4 (15.6)	86.9 (16.6)
	C	L	C	L	C	L	C	L	C	L	C	L

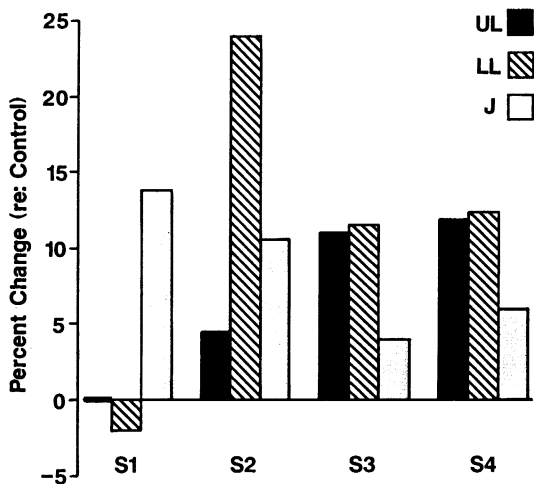


Fig. 3. Movement duration changes with load for the UL, LL, and J for all subjects expressed as a percent increase or decrease (re: control)

Peak velocity timing relations

To examine the effects of load perturbations on speech movement coordination, the UL, LL, and J peak velocity timing relationships were analyzed. Presented in Fig. 4 are scatter plots relating the time of peak velocity for the UL-LL, UL-J, and LL-J for the load and control conditions from subject 3. As can be seen, the relationship of the UL-LL, UL-J, and LL-J in the unperturbed condition are maintained following the application of the load; however, it can also be seen that variability in the peak velocity timing relations is increased. In order to quantitatively examine these relations, individual linear regressions were obtained for the UL-LL, UL-J, and LL-J times of peak velocity for the two

conditions. The slope coefficients relating the peak velocity timing of each articulator pair were statistically compared. Table 2 presents the results of the slope comparisons and the coefficient of determination (R^2) for the UL-LL, UL-J, and LL-J peak velocity timing relations for all subjects. Most importantly, the slopes of the regression lines relating any two articulator peak velocity times were generally similar for the two conditions. As can be seen, only 5 of the 12 load-control slope comparisons reflect a statistically significant difference at $p < 0.05$ (two-tailed test) with only the UL-LL and LL-J load/control comparison for S2 significantly different at $p < 0.01$. As shown, the UL-LL and LL-J relations were the most affected by the LL perturbation. The modest increase in variability with load, evidenced by the reduction in R^2 for articular pairs, was a consistent finding for all subjects. The average increase in the variability of the UL-LL, UL-J, and LL-J peak velocity timing relations was 13%, 9%, and 5%, respectively. In contrast to the consistent compensatory displacement adjustments for oral closure the peak velocity timing and movement durations changes were more resistant to change.

One aspect of the velocity profiles for the three articulators was maintained in the presence of LL loads. As mentioned, the timing of peak velocities for the UL, LL, and J has been shown to be consistently ordered (Gracco and Abbs 1986); the UL peak velocity occurs before the LL peak velocity which occurs before the J peak velocity. This consistent sequencing was maintained in the present study. Of the over 360 responses (load and control), only 14 (10 load, 4 control) were reversed from this sequence (i.e., LL before UL, etc.). Figure 5 illustrates the sequencing and average relative times of peak velocity for the UL, LL, and J in the control and load

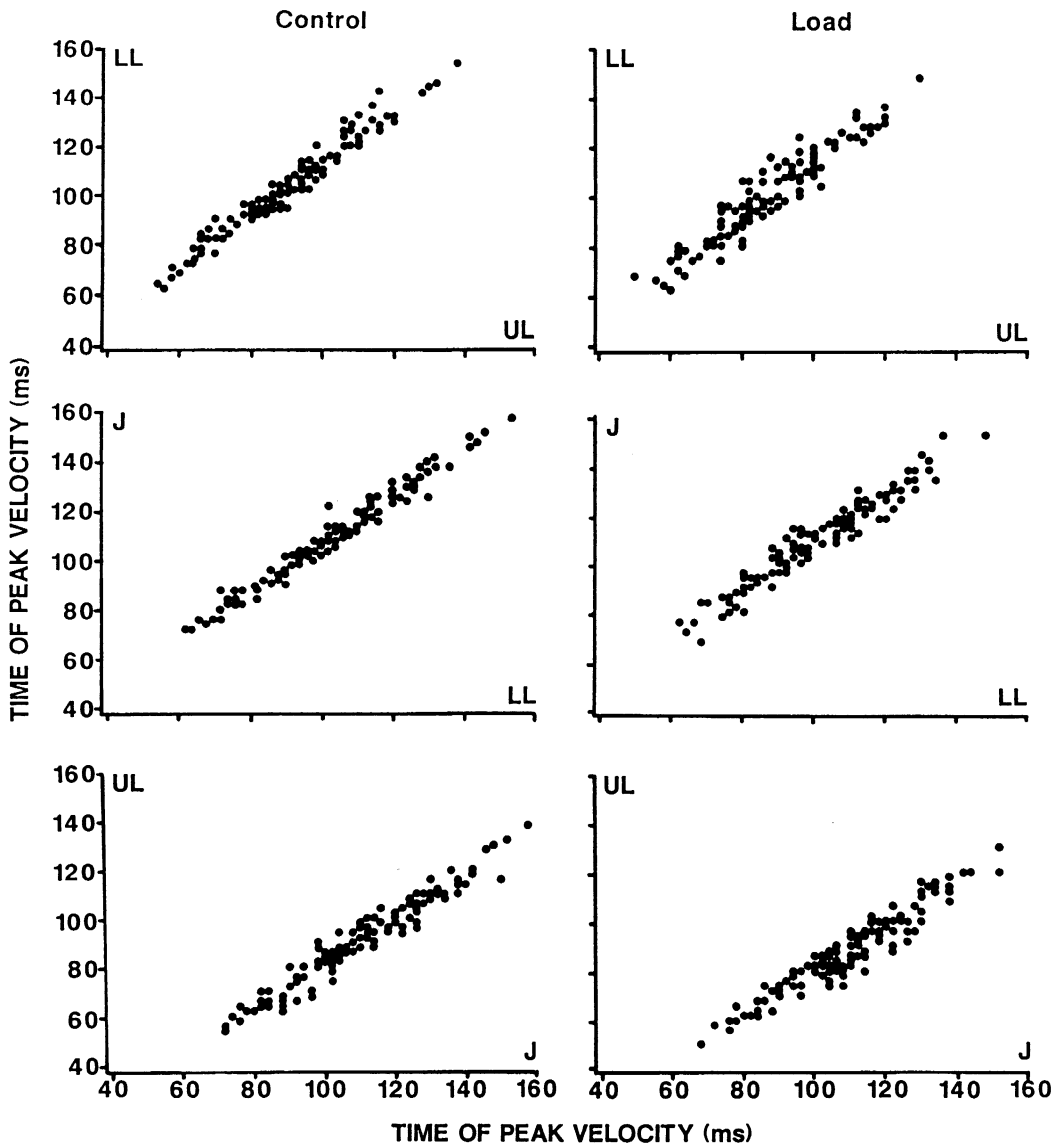


Fig. 4. Scatter plots of the peak velocity timing relations for each articulator pair; the UL-LL, LL-J, and J-UL from subject 3 for the control and load conditions. Individual times of peak velocity (relative to jaw opening peak velocity) were obtained and subsequently evaluated using linear regression to determine the slope relations among the articulator pairs (see Table 2)

Table 2. Comparison of regression slope coefficients indicating the relationship between articulator pairs for control and load conditions. The linear slope coefficients for each pairing (UL-LL, UL-J, LL-J) were compared statistically to determine if timing relations among articulator velocities were scaled from control to load conditions. Numbers in parentheses reflect the coefficients of determination for the individual regressions. * = $p < 0.05$; # = $p < 0.01$, for two-tailed test

	Control			Load		
	UL-LL	UL-J	LL-J	UL-LL	UL-J	LL-J
S1	1.03(0.93)	0.93(0.96)	0.83(0.92) n = 72	0.93(0.86)	0.92(0.92)	0.86(0.87)
S2	0.95(0.91)	1.04(0.94)	1.05(0.96) n = 63	1.11(0.86)	1.05(0.94)#	0.86(0.89)#
S3	0.93(0.85)	0.87(0.81)	0.91(0.80) n = 114	0.92(0.68)	0.85(0.70)	0.82(0.80)
S4	0.86(0.88)	0.81(0.83)	0.93(0.93) n = 117	0.70(0.65)*	0.64(0.63)*	0.84(0.80)*

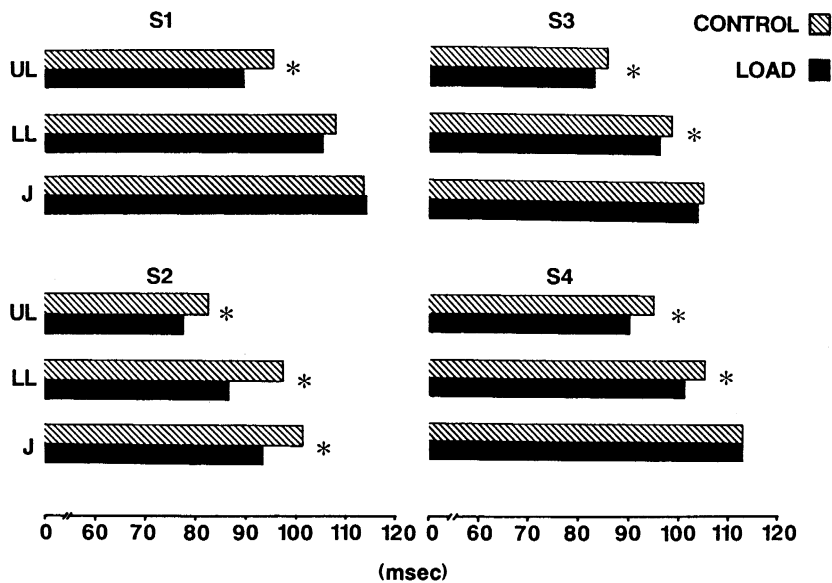


Fig. 5. Bar plots illustrating the average sequence of occurrence of the UL, LL, and J peak velocity for the for all subjects. Cross-hatched lines indicate the control condition, filled-bars indicate the load condition. All times are relative to the maximum jaw velocity associated with the opening movement for the first 'a' in 'sapapple'

conditions for all subjects. As shown, the ordering of peak velocities (relative to jaw opening peak velocity) is maintained following perturbation.

Although the peak velocity sequencing was maintained, the relative time of peak velocity changed for three of the four subjects (Fig. 5). That is, the time of peak UL and/or LL *closing* velocity relative to jaw *opening* peak velocity was found to occur significantly earlier with load for all subjects ($p < 0.05$). In contrast, the time of jaw closing peak velocity was generally unaffected with the exception of subject 2. Presumably, the relative time of peak jaw closing velocity may not be as crucial to the overall coordination. It may only be important that the jaw peak velocity occurs following the UL and LL peak velocity. Together, the consistency of the peak velocity sequencing and the relative timing relations among articulators are important components of speech movement coordination. Further, the earlier occurrence of the time of peak velocities for the UL and LL suggests a change in the underlying muscle action.

Muscle activity changes

To investigate the muscular changes associated with LL perturbation, EMG magnitude and temporal parameters were analyzed in detail. Load-induced changes were observed in EMG area from a least three of the four muscles analyzed, including the J muscle from S1 ($p < 0.05$; t-test for paired data). Changes in peak EMG amplitude were more variable. All LL and J muscle peak amplitudes increased

significantly while only one UL muscle for S1, S3, and S4 demonstrated a significant increase ($p < 0.05$). The EMG magnitude changes were not as robust as previously observed (Abbs and Gracco 1984); however, in the present study, the J was free to contribute to the compensatory action, providing another degree of movement freedom. It appears that increasing the degrees of compensatory freedom distributes the compensatory action.

Consistent with the kinematic changes reported above, muscle timing changes were also observed following LL perturbation. Specifically, the earlier occurrence of UL and LL peak velocity was accompanied by earlier EMG onset and time of peak EMG amplitude (re: jaw opening peak velocity). This can be seen qualitatively in Fig. 6 with three load/control trials from subject 3. For all subjects, all EMG onsets occurred earlier in response to the load, although only 9 of the 16 changes were statistically significant ($p < 0.05$); 6 of the 9 were from LL muscles. In addition, the time of peak EMG also occurred earlier for 14 of the 16 muscles (8 significant at $p < 0.05$; 4 from LL muscles). Because of the concomitant change in EMG onset and relative time of peak EMG, the duration of the rising phase of EMG activity (the difference between time of peak EMG and time of EMG onset) was used as an indicator of change in the EMG pattern. The time to reach peak EMG for the UL and LL muscles for the two conditions is presented in Fig. 7. As can be seen, the time to reach peak EMG was inconsistently affected by the load. While a tendency can be seen for a decrease in rise time (presumably reflecting an increase in firing frequency), only two comparisons

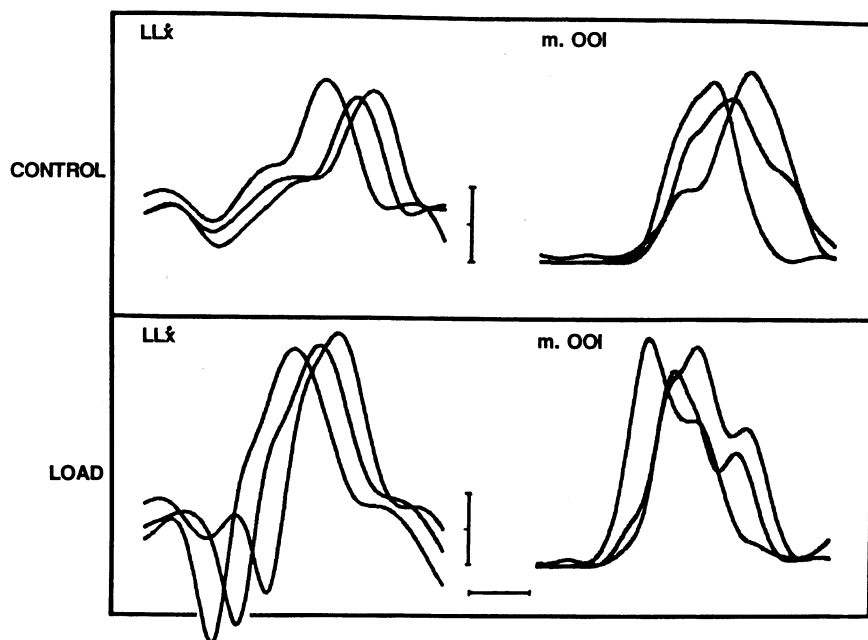


Fig. 6. Three pairs of load and corresponding control trials from subject 3 illustrating the changes in LL peak velocity and muscle activity (m. OOI). Load induced displacement of the LL is reflected in the negative portion of the velocity profiles. In general, earlier occurring velocity peaks are associated with earlier onset of muscle activity. All trials are aligned to jaw opening peak velocity. EMG activity was low-pass filtered at 20 Hz for illustrative purposes. Vertical bars indicate + and -50 mm/s with the midpoint representing 0 velocity. Horizontal calibration is 50 ms

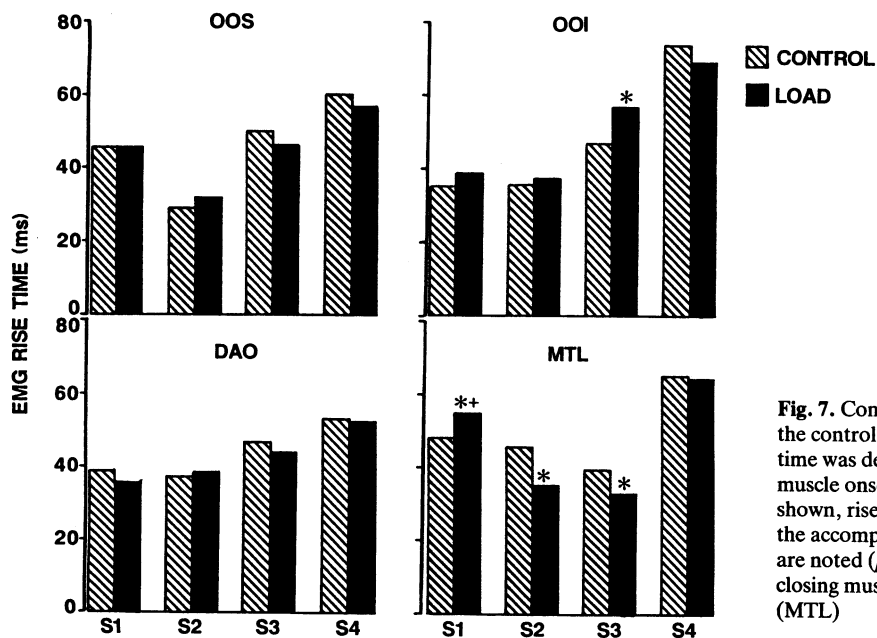


Fig. 7. Comparison of the average EMG rise times for the control and load conditions for all subjects. Rise time was defined as the time between the identified muscle onset and the time of peak EMG amplitude. As shown, rise times did not exhibit consistent trends for the accompanying compensation. Significant changes are noted ($p < 0.05$); + for S1 indicates data from a jaw closing muscle (MPT) rather than a lower lip elevator (MTL)

(MTL for S2 and S3) reflected significant changes; two comparisons can be seen to increase significantly. An ensemble average of the EMG from an UL, LL, and J muscle from subject 1 is presented in Fig. 8. It can be seen that the timing of the onset and the peak EMG amplitude occurs slightly earlier. Additionally, the J muscle activity does not reflect an earlier onset. The overall increase in J muscle activity is consistent with the lack of J peak velocity changes observed for most subjects. Considering that

most muscles demonstrated no significant increase in EMG rise time with load, similar times to reach peak EMG suggest that the compensatory EMG adjustments were often amplitude scaled versions of the unperturbed muscle patterns.

Discussion

The present investigation was undertaken to determine if certain consistent timing relations among the

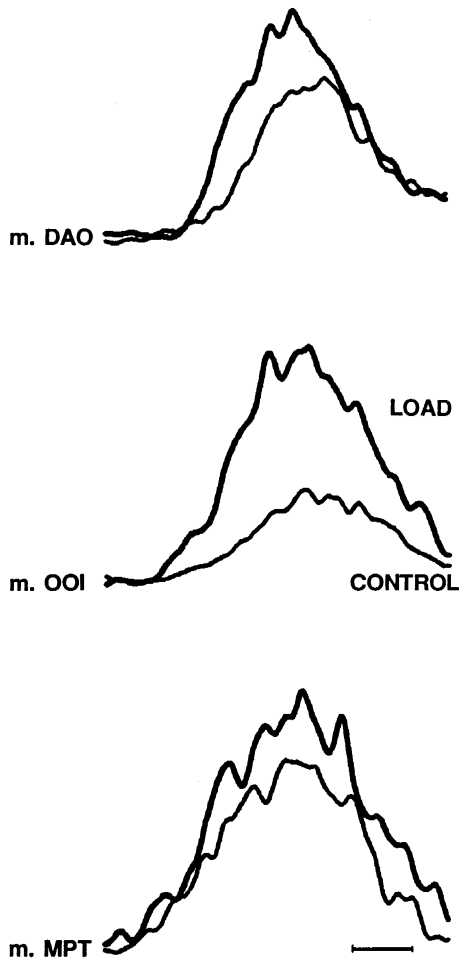


Fig. 8. Ensemble average ($n = 72$) of an upper lip muscle (m. DAO), lower lip muscle (m. OOI), and jaw closing muscle (m. MPT) illustrating the load/control changes in muscle activity. Thick and thin lines indicate load and control, respectively. The tendency for a general scaling of the EMG patterns can be seen qualitatively. Horizontal calibration is 50 ms

movements of the UL, LL, and J would be maintained in the presence of a potentially disruptive event. Comparison of the load and control results suggest that the sequencing of the UL, LL, and J peak velocities observed during unperturbed oral closure was maintained following LL perturbation. To a lesser extent, relative timing among the articulators reflected a tendency to scale timing adjustments following lower lip perturbation to the control condition. As with previous studies (Abbs and Gracco 1984; Gracco and Abbs 1985), lower lip perturbation resulted in distributed displacement adjustments in the UL, LL, and J movements to achieve the necessary oral closure. The tendency to minimize movement durational changes is in contrast

to previous results in which UL and LL movement durations for oral closing were found to increase significantly (range 26% to 50%) for all subjects (Gracco and Abbs 1985). The previous study, however, examined a single multiarticulate closing movement (aba) rather than a closing movement in the context of a word requiring multiple sequential adjustments. Within this sequential movement context, movement duration changes appear to be minimized, apparently to maintain the temporal relations of subsequent coordinative adjustments. It can be concluded that the consistent sequencing and timing of speech movements are critical components of speech movement coordination facilitating the achievement of the speech movement goal.

One difference in the present study from previous investigations of perturbation responses during grasp, rapid limb movements, and speech involves time-dependent patterns of compensatory changes (Cole and Abbs 1987; Day et al. 1983; Gracco and Abbs 1985). Specifically, time-dependent compensatory adjustments have been observed in which the pattern of response varies with the timing of load application relative to the onset of voluntary muscle activity. For speech, load timing variations have been shown to have systematic effects on the site (UL vs. LL) and magnitude of the compensatory speech movement adjustments (Gracco and Abbs 1985). In the present study, these trends were also observed for UL and LL displacement changes; however, movement duration and the velocity timing measures were only generally affected by load onset timing. That is, for loads occurring as early as 120 ms before and as late as 40 ms after EMG onset, the magnitude of change in movement duration or peak velocity timing was not dependent on the timing of the load, only on the presence of the load. The lack of time-varying load onset effects suggests that certain aspects of speech movement coordination may reflect a central process involving patterned motor output to multiple synergistic muscles.

The earlier occurrence of UL and LL peak velocities is consistent with the expected effect of sensory input in phase with centrally-generated motor patterns (Kristan 1980). That is, somatic sensory signals from the LL perturbation interact with centrally driven motor impulses to produce a phase-advanced output seen as an earlier occurrence of peak muscle activity and, consequently, earlier times of peak velocity. This observation found for most muscles and resulting movements combined with the maintenance of the UL, LL, J velocity sequencing outlined above provide further evidence for a central pattern generator (CPG) underlying the rhythmic structure of episodic speech movements

(Gracco and Abbs 1986). Although data obtained from human studies do not allow for elucidation of the specific type or organization of neuronal pattern generators as proposed and elaborated for other motor behaviors (cf. Bentley and Konishi 1978; Kristan 1980; Stein 1978 for reviews), the present study provides some insight into certain characteristics of such a pattern generation process for speech.

Characteristics of pattern generation in speech movements

Speech is a time-dependent process involving rapid movements of the lips, jaw, tongue, velum, vocal folds, and respiratory system. To generate these phasic movements, some form of patterned neural impulses onto the relevant lower motoneurons is required. The compensatory adjustments to perturbation observed in the present study resulted in magnitude changes in muscle activity (peak EMG amplitude and EMG area), apparently incorporated into an existing muscle pattern. While not measured in the present study, the relatively small changes in movement duration suggests small changes in the total EMG burst duration. Further, the increase in peak EMG amplitudes and similar or shorter EMG rise times for the load condition suggest that increases in the extent of lip movements were primarily accomplished by adjusting the amplitude of the rising phase of muscle activity, thereby increasing the number and frequency of motoneuron firing. While changes in the duration of the centrally generated motor pattern must have occurred (movement durations were generally longer), the time interval for the initial rising phase of muscle activation was not significantly modified. It appears that one component in the organization of speech movements is a motor pattern of specified rise-time and duration. This is not to suggest that the duration of the rising phase or burst duration is necessarily the same for all muscles or conditions. As shown recently, internally generated variations in movement speed and timing can also be accomplished by a reciprocal variation in the duration and amplitude of the muscle activation pattern (Gracco 1986). That is, rapid oral closing movements are produced with relatively short duration, high amplitude EMG patterns; slow oral closing movements are produced with relatively long duration, low amplitude EMG patterns. Rather, it appears that a basic motor pattern can be scaled differently (amplitude and/or time) to produce a variety of kinematic events specific to the speech task.

An additional hypothesis regarding speech move-

ment coordination is that the timing of each structure (UL, LL, J) may be differentially influenced in a task-specific manner by separate inputs onto the CPG. The observation of task-specific UL, LL, J, or tongue responses to lower lip or jaw perturbation (Abbs et al. 1984; Folkins and Abbs 1975; Kelso et al. 1984) and the ability to produce "f" and "v" sounds with little or no UL activity suggest that the UL muscles can be functionally decoupled from the coordinative pattern. Further, the inconsistency of the J peak velocity timing changes in comparison to the consistently earlier UL and LL peak velocities (Fig. 5) suggests that for sounds produced with UL, LL, and J actions, the UL and LL may function as a unit with their action superimposed upon a more basic J pattern. Given the strong evidence for a brain stem pattern generator underlying rhythmical mastication, it is plausible that opening-closing movements of the jaw during speech may rely on the same circuitry or mechanism as has been proposed for chewing (Dellow and Lund 1971; Lund and Dellow 1969; Sumi 1969). Finally, the observations of inter-subject differences in the UL, LL, and J *opening* velocity sequencing (Gracco 1986; Gracco and Abbs 1986) as well as recent evidence for different, but consistent, closing velocity sequencing in individuals who stutter (Caruso et al. in press) suggest that each articulator can be driven independently, apparently relying on a "higher level" process for their coordination (see also, Grillner 1982).

A final comment on hypothetical processes underlying speech movement coordination. The suggestion that speech production may involve such rhythm generating processes (central pattern generators, network oscillators) should only be considered tentatively. As shown in the present study, speech movement coordination is subject to multiple influences and displays a degree of variability not often seen when investigating CPGs or other rhythmic mechanisms found in spinal preparations or organisms with simpler neural systems. The degree of variation and lack of invariant relations often observed in more complex motor behaviors such as speech may reflect a lack of similarity in fundamental mechanisms for such diverse rhythmic motor actions as stepping, scratching or chewing. Further, it is difficult to compare results obtained from direct cellular recording of limited numbers of neurons to the observables dealt with in human behavioral studies. Conversely, if the present results can be taken as suggestive of an underlying process for the temporal coordination of speech movements there is a need for modification or elaboration of extant neurophysiological mechanisms to accommodate the more variable motor behaviors such as speech.

Neurophysiological bases of speech movement patterning

The results from the present study emphasize the importance of timing relations among multiple movements for their coordination. While limited neurophysiological information is available on the specific neural processes of speech movement coordination, some consistent findings from non-speech behaviors in lower vertebrates allow for limited speculation. For episodic or rhythmic multiarticulate movements, the pattern generator must be activated at the appropriate time and the output must be scaled to the appropriate task requirements (e.g., magnitude and speed). Based on lesion and stimulation studies, the lateral nonprimary motor area has been implicated in the activation of the patterned movements for swallowing, chewing, and lapping (Larson et al. 1980; Lund and Lamarre 1974; Luschei and Goodwin 1975; Magoun et al. 1933; Sumi 1969). The cortical influences on the brainstem CPG would allow for the fractionation of the more innate motor behaviors; the hard-wired circuitry could then be manipulated to accommodate the variable speech production process (cf. Grillner 1982; Netsell 1982). The cortical and subcortical orofacial representation and interconnections of multiple neural centers would allow the flexibility for adjustment in the magnitude and task-specific articulator timing requirements for speech movement coordination. The result of such a representation is that the interaction of multiple processes and presumably multiple brain regions, is synthesized to produce an extremely stable and invariant motor output. Further, no single neural process would necessarily reflect the end product (e.g., systematic spatial or timing adjustments); rather, the parts combine in a complex but consistent manner to produce the observed movement invariance.

Sensory interaction with speech motor output

The interaction of sensory information with patterned speech motor output can be considered from two perspectives: sensory influences on the (1) magnitude and (2) timing of speech movements. As in previous studies, compensatory changes in movement displacement were observed in all contributing structures (Abbs and Gracco 1984; Folkins and Abbs 1975; Gracco and Abbs 1985; Kelso et al. 1984). Compensatory movement adjustments distributed among the multiple articulators suggest a complex interrelationship among speech structures in which modification of one structure involves modifications

of all functionally-linked structures. However, as demonstrated previously, articulator interactions are not stereotypic or consistent from repetition-to-repetition. Rather, multiarticulate speech movements reflect systematically variable distributed adjustments reflecting an interdependency related to the motor goal of oral closure (Gracco and Abbs 1986; Saltzman 1986). While recent investigations have begun to identify some general consistencies among the multiple speech movements (Folkins and Canty 1986; Folkins and Linville 1983), the specific relations are yet to be determined. However, the present results strongly suggest that for speech, as for other patterned motor behaviors, sensory signals can be used to scale the basic motor patterns underlying the multiple muscles and movement adjustments. Once adjusted, the motor patterns are apparently "fine-tuned" by on-line sensorimotor mechanisms (Abbs et al. 1984; Gracco and Abbs 1985).

The earlier onset of muscle activity with load indicates that somatic sensory influences can interact with centrally generated motor patterns to modify the timing of motor output. This is in contrast to locomotion studies in the cat in which peripheral stimuli, or lack thereof due to deafferentation, do not lead to intralimb timing changes (Grillner and Zangger 1975). However, the earlier onset of muscle activity and the lack of significant EMG rise-time changes reflect the limited effect that somatic sensory information has on speech movement timing. It appears that sensory-mediated UL and LL relative timing changes are limited to the onset of muscle activity, leaving the basic motor pattern and the relative velocity timing relations unchanged. Similarly, for speech movement sequences, it has recently been demonstrated that the presence or subsequent removal of a LL load results in reciprocal changes in the onset of subsequent muscle activity (Gracco and Abbs in press). Adjustment in muscle activation timing in response to a peripheral stimulus, however, does not imply that rate variations or movement initiation is entirely a peripherally mediated event. Rather, peripheral sensory input from a preceding movement has the potential to trigger subsequent movements or assist in maintaining movement rate across sequential movements. Finally, sensory-mediated J timing and magnitude adjustments are differentially affected by the LL perturbation. All subjects demonstrated J movement compensations while only one subject demonstrated J peak velocity timing changes. Apparently, sensorimotor interactions across the multiple movements differentially affect movement timing and magnitude adjustment.

As in locomotion, chewing, and other rhythmic motor behaviors, there appears to be a centrally

patterned framework for speech movements. These centrally patterned movements are not stereotypic since even repetitions of the same word have been shown to reflect systematic motor equivalence variations (Gracco and Abbs 1986; Hughes and Abbs 1976). Rather, as shown in this and the previous study, there are systematic relations among multiple movements consisting of a basic pattern of motor output which is scaled through sensorimotor interactions. The invariant features of speech motor control are the achievement of multiarticulate goals (e.g., lip closure) and the time-dependent coordination of the multiple articulators. A centrally-generated pattern of motor output, involving temporally asynchronous and consistently ordered input to the lower motoneurons, reduces the degrees of freedom to control, thereby facilitating the multiarticulate coordination. The finding that the load or load timing did not systematically affect the velocity sequencing suggests that sensory modification of timing is limited to the activation signal and, perhaps through summation, the rate of motoneuron recruitment. Once movement speed is specified and the basic motor patterns scaled, the critical timing relations allow for the successful achievement of the speech motor goal.

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