

Sensorimotor characteristics of speech motor sequences

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Summary. The present experiment focused on the characteristics of sequential speech movements. Subjects generated two successive lip and jaw closing movements associated with the two 'p's' in 'sapapple'. By selectively manipulating the lower lip perturbation it was possible to discern the role of somatic sensory interactions with the presumed sequential movement programming. Lower lip perturbation duration was manipulated to yield two different load conditions. In the Load On (LN) condition, the perturbation remained on for both closing movements. In the Load On/Off (LNF) condition, the perturbation was removed at variable times prior to the second closing movement. Analyses focused on comparing the EMG and resulting kinematic changes for the second "p" closure across the two load conditions relative to the normal control (no load) condition. The second "p" closure was differentially affected by the load conditions resulting in changes in the upper and lower lip compensations. Upper lip changes reflected consistent load duration differences; however, the magnitude of the lower lip EMG and kinematic adjustments did not mirror those of the upper lip. In contrast to the differential upper lip/lower lip changes observed for the magnitude adjustments, timing adjustments were similar for both upper lip and lower lip suggesting a separation between the specification of magnitude and timing of speech movements. Differential load effects were also observed for the timing of the second closing movements. For the LN condition, the onset of muscle activity and subsequent movement occurred earlier (re: control); for the LNF condition, load removal delayed the onset of muscle activity and the subsequent movement (re: control). Further, the

opening movement preceding the second closing movement was modified for both load conditions suggesting that all movements in the sequence, not just closing movements, can be modified. The present results suggest that the programming of speech movement sequences is a dynamic process involving scaling and timing of motor commands relying on various degrees of sensory interaction. The apparent separation in the magnitude and timing specification of the movement sequences suggests the parallel influences of different neural systems. The consequence of this control scheme is that specification of movement parameters for sequential motor acts is a flexible real-time sensorimotor process interacting with less-flexible well-established central motor relations. Further, motor programs for speech may reflect certain generalized movement actions (e.g., oral opening, oral closing) rather than individual words, syllables, or other linguistic categories programmed on a movement-to-movement basis.

Key words: Sensorimotor – Speech movements – Motor control – Motor programming

Introduction

Speech, typing, handwriting, and many other human activities involve the execution of sequential multi-articulate movements. The neurophysiological processes underlying these serial actions are of importance as these are some of the most skilled human motor behaviors. Over the years considerable research has focused on the neural representation of such sequential motor actions from a variety of perspectives including neurophysiological (Benecke et al. 1986; Schonle et al. 1986; Terzuolo and Viviani 1980), information processing (Gentner 1987; Stern-

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berg et al. 1978; Sternberg et al. 1980) and memory retrieval (Henry and Rogers 1960; Miller 1956). The issue addressed in many behavioral studies has been to determine the size, completeness, or other characteristics of the underlying motor commands for complex, sequential movements. Henry and Rogers (1960) were the first to illustrate that movement sequences required more initiation time following stimulus onset than single movements. Since then, numerous studies have demonstrated increases in reaction time with increases in response complexity for a variety of motor actions including morse code production, word repetitions, and handwriting (Klapp et al. 1973; Klapp and Wyatt 1976; Monsell 1986; Sternberg et al. 1978; Sternberg et al. 1980). Such findings have been interpreted to reflect conceptual processes such as the time required to "load" (Henry and Rogers 1960), "program" (Schonle et al. 1986), or "assemble" (Glencross 1972) the required motor commands. In general, reaction time results suggest that the control of sequential movements may involve different processes than those underlying simple movements.

Other investigations, however, suggest that the underlying motor representation for single versus sequential movements may be fundamentally similar. For example, from the consistent temporal relations among typing keystrokes, Terzuolo and Viviani (1980) have suggested that longer polysyllabic or compound words are composed of stored motor patterns reflecting letter segments rather than the individual words (see also Gentner 1982). In handwriting, likewise, producing a variety of letters and slants from orthogonal oscillators (Hollerbach 1981) or complex trajectories from simple strokes (Edelman and Flash 1988) suggest that the unit of representation may be some smaller component of the overall movement sequence (see also Mermelstein and Eden 1964; Morasso and Mussa-Ivaldi 1982). For more novel sequential motor tasks involving the upper limb, a lack of correlation between movement times for various movements in the sequence suggests that each movement is controlled separately (Benecke et al. 1986). These studies indicate that serial motor actions may involve sequencing of a limited number of basic motor actions adjusted for each movement. However, most studies of sequential motor actions have focused on the relative timing among the component movements. Only limited attention has focused on the magnitude adjustments of the multiple components that must also accompany the movement-to-movement sequential actions.

In this context, the present experiment focused specifically on the muscle contraction and kinematic parameters associated with sequential speech move-

ments. It has been demonstrated previously that if movement of one speech organ (e.g., the jaw) is unexpectedly perturbed prior to movement initiation, movements of other structures (the lip or tongue) are adjusted in a compensatory manner to achieve the intended speech goals (Abbs and Gracco 1984; Folkins and Abbs 1975; Gracco and Abbs 1985; Kelso et al. 1984). Further, these compensatory adjustments are time-dependent, reflecting the differential contributions of upper lip and lower lip adjustments during different movement phases (Gracco and Abbs 1985). However, previous speech perturbation studies have focused on single multiarticulate movements or have analyzed only the first movement in a longer sequence. Therefore, it was of interest to determine the capability to modify a portion of the sequence once the sequence has been initiated. By selectively introducing perturbations during different serial elements in a speech motor sequence, it was possible to discern certain characteristics of the presumed underlying motor command as well as the role of somatic sensory information in the production of the multiarticulate movement sequence. Results suggest that all components of a speech movement sequence are continuously modifiable by moment-to-moment sensory information. Further, the magnitude and timing of upper lip and lower lip compensatory responses were found to be differentially affected by the timing of load removal.

Methods

Subjects

Subjects consisted of five adult females between the ages of 22 and 26 years. All reported negative neurological histories and none exhibited speech difficulties. All subjects were naive to the objectives of the experiment and unaware of techniques or procedures in motor control studies.

Motor task

Subjects produced the word 'sapapple' (cf. Fig. 1) involving two successive lip and jaw opening/closing movements (P1 and P2, respectively) separated by the vowel 'ae'. Subject cueing was accomplished with an experimenter-controlled tone (1000 Hz, 250 ms duration) and subjects were requested to repeat the word 'sapapple' at a comfortable rate as if they were speaking to someone approximately 15 feet away. Electromyographic (EMG) activity was recorded from two upper lip depressor muscles (Orbicularis oris superior-OOS and Depressor anguli oris-DAO) and a lower lip elevator muscle (Orbicularis oris inferior-OOI) with hooked-wire electrodes. In one subject, EMG was also obtained from medial pterygoid (MPT), a jaw closing muscle. In parallel, vertical upper and lower lip/jaw movements were transduced in the midsagittal plane, using methods described previously (Gracco and Abbs 1986). EMG signals were bandpassed filtered

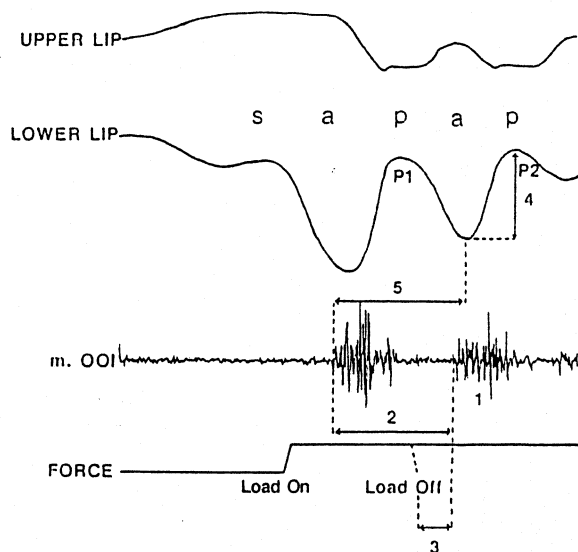


Fig. 1. Illustration of the experimental conditions and analysis scheme. Shown are the upper lip and lower lip movements and EMG activity from a lower lip muscle associated with the two "p" closing movements (P1 and P2) for "sapapple". In the Load On (LN) condition, a 45-gm force perturbation was applied to the lower lip for 1 s; in the Load On/Off (LNF) condition, a 45-gm force perturbation was applied to the lower lip for 200–250 ms; numbers reflect the measures obtained in the present study. 1 – integrated area of the bursts of EMG activity associated with the closing movements; 2 – interburst interval calculated as the time between the onset of P1 EMG to the onset of P2 EMG; 3 – load offset time (ms. re: OOI) indicating the time between the offset of the load and the onset of the second burst of muscle activity for P2; 4 – maximum displacement (mm) for the second closing movement; 5 – onset of the second movement (P2) relative to the onset of the first burst of muscle activity (OOI) associated with P1. See text for further details

(50–2500 Hz) and digitized (3200 sps, 12-bit resolution) using a DEC 11/44 laboratory computer; movements were digitized at 800 Hz with no pre-acquisition filtering. Prior to data analysis, EMG signals were digitally rectified. Movement signals were digitally filtered (20 Hz low pass, two-pole maximally flat, zero phase lag) following acquisition.

Load perturbation technique

Using methods described previously (Abbs and Gracco 1984), inferiorly-directed load perturbations were applied to the lower lip prior to the closing movement for the first 'p' in 'sapapple'. Load magnitude was 45 gms and loads were applied on 15% of the speech movement trials. Each perturbed trial was associated with a corresponding control trial acquired from the unperturbed trial immediately preceding the perturbation. For the perturbed trials, the load duration was manipulated yielding two different conditions. For the Load On (LN) condition, the perturbation was one second in duration while for the Load On/Off (LNF) condition, the perturbation duration was 200 ms for four subjects and 250 ms for one subject. In the LN condition the perturbation remained on for the entire movement sequence (i.e., both P1 and P2 labial

closures), while in the LNF condition the load was removed prior to the second closure (P2). With this paradigm, it was reasoned that the manner in which these two load duration conditions influenced the second 'p' closure (P2) would reflect on the character of the underlying motor commands. For each subject, approximately 50 trials for each load condition were obtained, along with a corresponding number of control trials. Load onset was not time-locked to any speech event and was controlled by the experimenter. In general, an attempt was made to initiate the load onset prior to the onset of the OOI EMG activity associated with the first 'p' movement.

Data analysis

Comparison of the control and load conditions was accomplished by quantifying EMG and movement measures as described below. As shown in Fig. 1, the following measures were made:

- 1) area of the rectified muscle activity associated with P1 and P2.
- 2) time interval between the onset of P1 and P2 muscle activity (P1–P2 interval),
- 3) time from load offset (LNF condition) to the onset of P2 EMG (load offset time),
- 4) P2 upper and lower lip movement displacement (onset to peak),
- 5) time of P2 movement onset (re: P1 OOI onset).

EMG onsets were visually identified by a research assistant unaware of the different perturbation conditions. EMG onsets not clearly identifiable due to excessive background activity were not included in the analysis (comprising less than 3% of the total utterances). Movement onsets and offsets were identified from the first derivatives and defined as the time when the velocity trace for the closing movement increased or decreased to 10% of the peak closing velocity, respectively.

Results

Consistent with earlier reports (Abbs and Gracco 1984; Gracco and Abbs 1985) analysis of the first 'p' closure (P1) yielded statistically significant increases in EMG activity and the resulting movements for both load conditions ($P < 0.01$; paired-t). The most consistent finding across all subjects was differential adjustments in the magnitude and timing of the second closing movement associated with the two load conditions. Shown in Fig. 2 are representative single trials of lower lip muscle EMG for the two load conditions (Fig. 2-top, Fig. 2-bottom; the different load durations are indicated by the solid horizontal line) and a corresponding control condition (Fig. 2-middle). For the LN condition (2-top), compensatory EMG changes are substantial for P1 and P2. By contrast, in the LNF condition (2-bottom), the P1 EMG magnitude is increased while the P2 activity is similar to that of the control condition. In parallel there are apparent changes in EMG timing. Specifically, the onset of P2 EMG activity occurs earlier (re: control) for the LN condition (2-top), while P2 onset

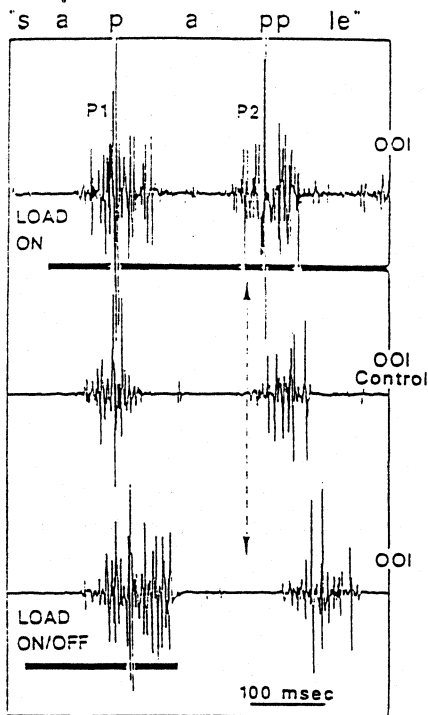


Fig. 2. Representative results from the autogenic lower lip muscle (OOI) for subject one demonstrating the EMG area and timing changes associated with the two load conditions for the second "p" (P2) in "sapapple". Shown is an unperturbed response (middle) and a single trial representing each of the load conditions: top-LN condition, bottom-LNF condition. EMG signals are lined up to the onset of the first burst of EMG activity associated with the first closing movement (P1). The dotted vertical line is a reference to the timing of the onset of the second burst of muscle activity for P2 (control) response. The horizontal line represents the load duration. The continued presence of the load on the lower lip results in an earlier onset of lower lip EMG activity. Conversely, the removal of the load prior to the second closing movement results in a delay in the onset of the lower lip EMG activity

is delayed following early load removal (2-bottom). In the results that follow all analyses presented will refer to the second closing movement, unless otherwise indicated.

Magnitude adjustments

The EMG and kinematic magnitude differences for the two load conditions were evaluated quantitatively. Shown in Fig. 3 are the average EMG area and movement displacement changes for the lower and upper lips for each subject. To allow for inter-subject comparisons, muscle activity and movement displacement changes have been converted to percent change of the control condition. As shown in Fig. 3 (top), the different perturbation conditions

(LN-LNF) resulted in differential changes in EMG integrated area. The average LL (OOI) EMG changes (Fig. 3, upper left) for the LN condition were significantly greater than the EMG changes associated with the LNF condition ($P < 0.01$; Student's t-test) with both conditions (LN/LNF) significantly greater than control ($P < 0.01$; paired-t). Similarly, LL movement compensation (Fig. 3, lower left) for the LNF condition was significantly reduced from the LN conditions for all subjects and significantly increased from the control condition for all but subject two ($P < 0.05$ for both comparisons).

In order to compare the UL results more completely, the results from both upper lip muscles recorded (OOS and DAO) were converted to a percent change (re: control) and summed. In contrast to the results from the LL, only three subjects demonstrated UL LN/LNF differences (subjects 1-3). Further, the LNF condition resulted in average UL EMG changes similar to or less than the unperturbed, control condition (Fig. 3, upper and lower right panel) apparently indicating a more complete readjustment to load removal. In contrast to the large LL compensation, the UL muscle and movement changes in the LN condition were less pronounced. For the LN condition, UL muscle changes ranged from -12 to 40% (re: control) for OOS and -27 to 65% for DAO. Upper lip movement changes (Fig. 3, lower right panel) similarly reflected less compensation than the LL for both load conditions.

Closer inspection of the UL EMG and movement changes reveal a potentially confusing result. For the LN condition, four of the five subjects demonstrate movement compensations that are unchanged or less than control values. At first glance it appears that the UL did not compensate for the lower lip load, a different result than reported in previous studies of upper lip compensation to lower lip loads (Abbs and Gracco 1984; Gracco and Abbs 1985). Further, the average change in EMG activity with load is somewhat contradictory to the observed kinematic results. For example, subject three has an average net decrease in EMG area with a concomitant average increase in UL movement. Conversely, subject two has net increase in UL EMG with no apparent UL movement compensation. While it is true that the relations between EMG area and the accompanying kinematic adjustments are not necessarily straightforward, the lack of significant UL movement changes is confusing. However, inspection of ensemble averages of the upper lip movement from the onset of the first closing movement to the completion of the second closing movement reflects a form of compensation not reported in previous studies. As shown in Fig. 4, the opening movement preceding

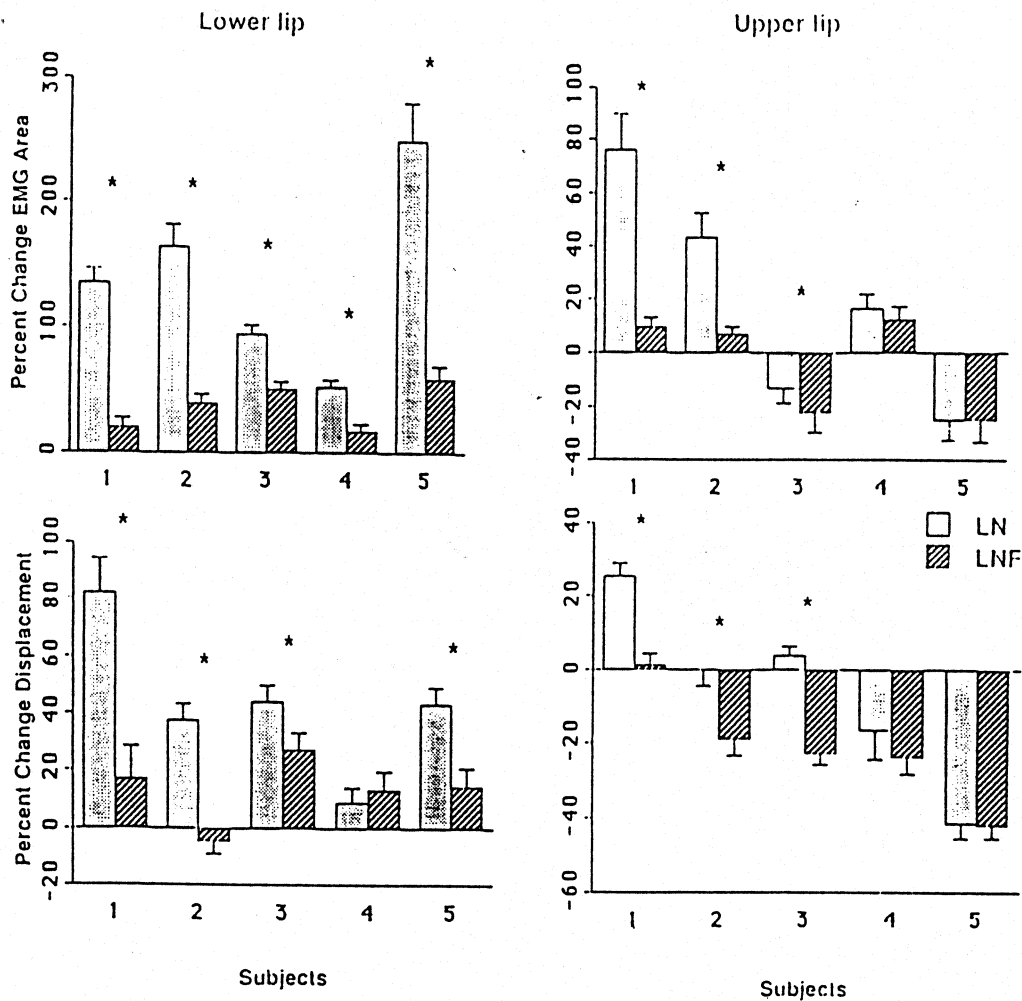


Fig. 3. Summary of the EMG area and movement displacement changes for the lower lip (left panels) and upper lip (right panels) for all subjects. EMG area and displacement changes have been converted to percent change (re: control). The lower lip muscle changes are from OOI while the upper lip muscle changes are from the sum of DAO and OOS. The different load conditions are identified in the legend; significant LN/LNF differences are indicated by the * ($P < 0.05$). The number of responses obtained from each subject per condition is as follows: Subject 1 - Control(C) = 84, LN = 38, LNF = 46; Subject 2 - C = 86, LN = 38, LNF = 48; Subject 3 - C = 120, LN = 54, LNF = 66; Subject 4 - C = 102, LN = 44, LNF = 58; Subject 5 - C = 112, LN = 53, LNF = 59

the second closing movement is reduced from the no load condition effectively reducing the extent of UL depression necessary for the second 'p' closing. Although relative displacement does not increase significantly and is even less than control values, the UL position at closure would be lower and in fact would assist the lower lip in the overall compensation. This pattern of reduced extent in the opening movement was observed for all subjects except subject one.

Timing adjustments

The interval between P1 and P2 (cf. measurements in Fig. 1) was also influenced differentially by the two

load conditions. In general, the LN condition resulted in earlier onset of muscle activity, while load removal resulted in an apparent delay in EMG onset. As shown in Fig. 5 for the LN condition, the P1-P2 (EMG interburst) interval was shorter than control values for all subjects while the interburst interval for the LNF condition was longer for three subjects and shorter in two. The inter-subject variation in the LNF condition appears to be directly related to variations in distribution of load offset times. Specifically, load offset times for subjects 1, 2 and 5 averaged 120, 70, and 100 ms prior to P2 EMG onset, respectively. By contrast, mean load offset times for subjects 3 and 4 occurred closer to P2 onset, averaging 50 and 40 ms prior to P2 EMG onset. It appears that the differing

Upper Lip

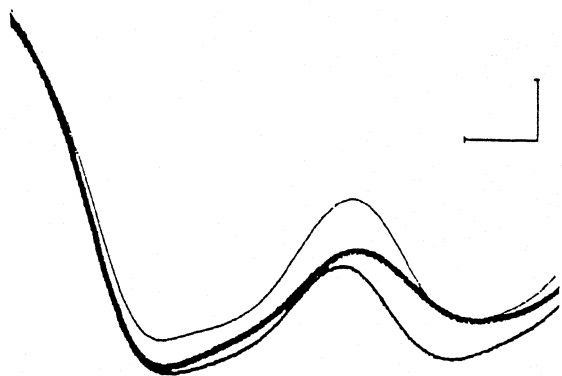


Fig. 4. Ensemble average of the UL movements for the two 'p' closing movements (P1 and P2) for 'sapapple' from subject 2. Closing is reflected in the downward direction while the opening movement for the 'a' in 'apple' is reflected by the upward movement. Each condition is represented by a different line thickness; the thinnest line is the control condition, the thicker line is the LN condition, and the thickest line is the LNF condition. As shown, the opening is reduced in the extent of movement relative to the control condition for both LN and LNF conditions. The amount of displacement required for closure is effectively reduced by the extent of opening. The resulting upper lip movement is increased in terms of the final spatial location even though the relative displacement is unchanged. Horizontal calibration is 50 ms; vertical is 2 mm

degrees of LN/LNF load condition changes may be dependent on the relative time of load removal. The potential load offset timing effects will be examined in detail in the following section.

The timing of the second closing movement (P2) also demonstrated consistent LN/LNF differences. Shown in Fig. 6 are the movement onset changes for the UL (top) and LL (bottom) for the two load conditions; four of the five subjects demonstrated statistically significant differences in the LN versus LNF conditions. As shown, movement onset for the second closing movement generally occurred earlier in the presence of the lower lip load (LN) and generally occurred later following load removal (LNF). Although consistent LN/LNF differences can be seen, the movement onset changes are not as robust and somewhat inconsistent with the LL EMG timing changes presented in Fig. 5. This could be related to multiple factors including difficulty in identifying EMG onset, the presence of the load obscuring the movement onset, and the tenuous assumption that EMG onset is related in a simple and consistent way to movement onset. It appears that although muscle timing is modified, the resulting movement onset is less affected; UL movement onset changes were more consistent with the UL EMG changes. In general, the onset of the second closing

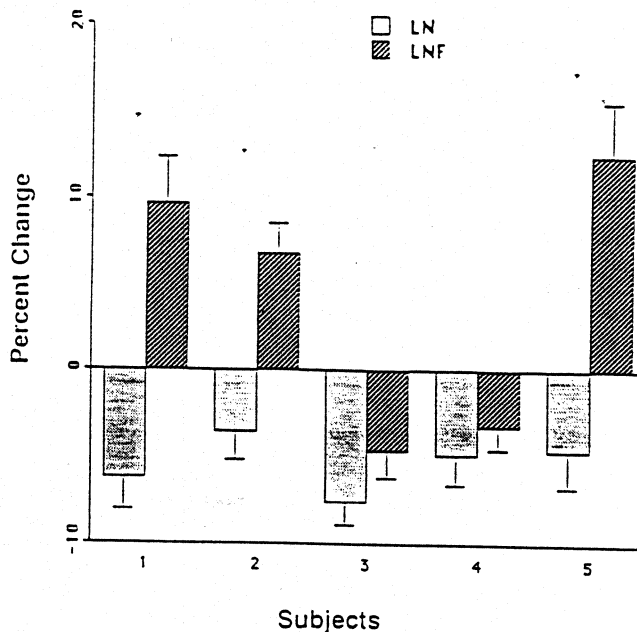


Fig. 5. Summary of the mean interburst intervals for the load conditions for the lower lip muscle (OOI), expressed as a percent increase or decrease from the control (no load) condition. Significant LN/LNF differences are indicated by the * ($P < 0.05$). As shown, removal of the load (LNF) resulted in a delay in the onset of the muscle activity for the second closing movement

movement was similarly modified for the upper and lower lips.

Load offset timing changes

In order to examine the influences of load offset timing in detail, magnitude and timing changes for the LNF condition were pooled across subjects and analyzed. The EMG magnitude data, expressed as a percent change (re: control) were averaged for the five 50 ms intervals ranging from 200 ms prior to P2 EMG onset to 50 ms following P2 EMG onset. Because the magnitude of LL EMG change from subject 4 in the LN condition (mean = 52.6%) was substantially less than the other four subject, and inclusion of these data appeared to distort the group LN mean used as a reference, the individual data from this subject were not included in this analysis. Further, to minimize effects related to load onset time differences, only LN trials with load onset times (re: EMG onset for the first closing movement) occurring within 100 ms of P1 EMG onset were included in the comparison. Therefore, the mean for the LN condition, used as a reference, is similar to but not the same as would be expected from Fig. 3. In general, the contingencies established for inclu-

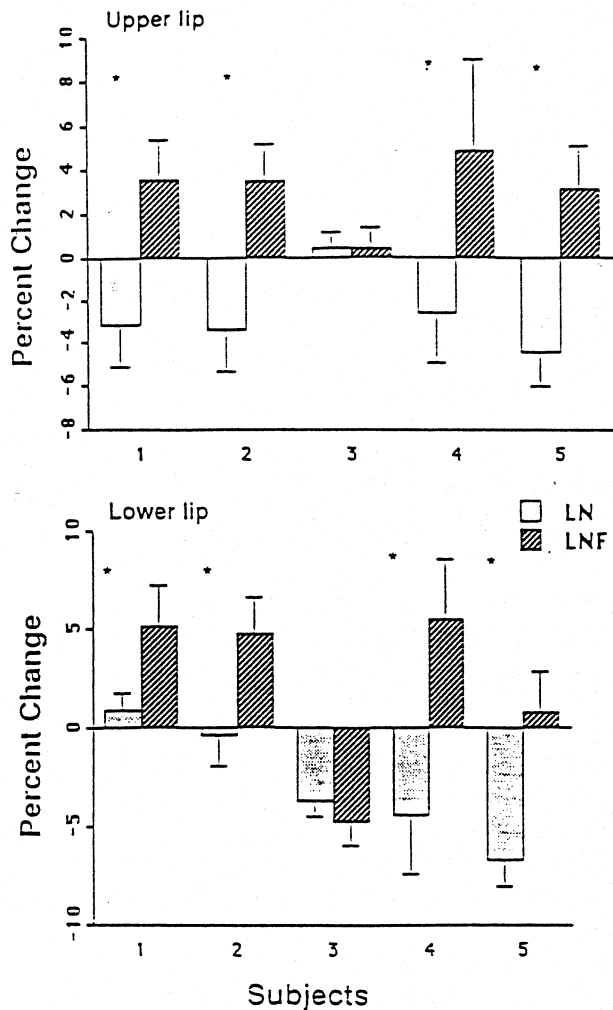


Fig. 6. Summary of the UL and LL movement onset changes for the second closing movements (P2), expressed as a percent increase from the control, for the LN and LNF conditions. Significant LN/LNF differences are indicated by the * ($P < 0.05$). Similar to the EMG findings presented in Fig. 5, the presence of the load resulted in earlier onset of the closing movement while a delay in movement onset occurred following load removal

sion of pooled data resulted in a more homogeneous data set less subject to individual subjects influences. It should also be noted that the trends observed for the group data are representative of all subjects. Figure 7 (top) illustrates the change in EMG magnitude for the LNF condition as a function of the load offset timing. The average increase in OOI EMG magnitude for the LN condition (128% , ± 1.0 SE) is shown by the cross-hatched zone. As shown in Fig. 7 (top), with later removal of the load, LL EMG changes are more similar to those obtained when the load remained on (LN condition).

There are three results of particular note in Fig. 7 (top). First, even when load offset occurred as late as

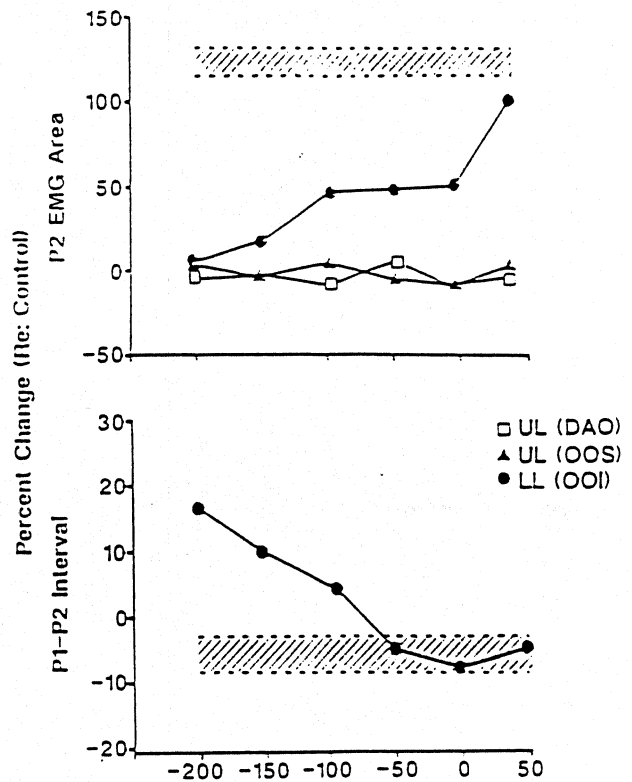


Fig. 7. P2 EMG area changes for the LL (OOI) and UL (DAO and OOS) (top) and P1-P2 interval changes for the LL (OOI) (bottom) as a function of load offset time for the LNF condition. The horizontal axis reflects the load offset time (in ms) relative to the onset of the P2 EMG activity for the lower lip muscle (OOI); a negative number reflects load offset time before P2 onset, a positive number reflects load offset time after P2 onset. Responses from the subjects were pooled and averaged according to load offset time intervals (Re: P2 onset) of approximately 50 ms. Stippled area reflects the group average for the lower lip muscle (± 1 S.E.) for the LN condition: upper lip muscle averaged 19% for the LN condition; 0% reflects the control (no load) condition. For the P1-P2 interval (bottom), the early load offsets (200 to 100 ms before P2 onset) were significantly longer than both the controls and the LN average ($P < 0.05$); later load offsets (50 ms before to 50 ms post P2 onset) were significantly shorter than the control condition ($P < 0.05$) but not different than the LN condition ($P > 0.05$)

40 ms after EMG onset, the EMG area changes are less than the LN condition. For loads removed even later, the average EMG increases parallel the LN condition suggesting that the EMG can be modified well after onset. Secondly, even when the load was removed as early as 150 ms prior to EMG onset, the EMG area changes were greater than the (no-load) control condition. This latter result suggests that while considerable modification is possible with changes in peripheral condition, some aspect of sequential EMG activity may not be sensitive to peripheral changes. Finally, as shown by the lower

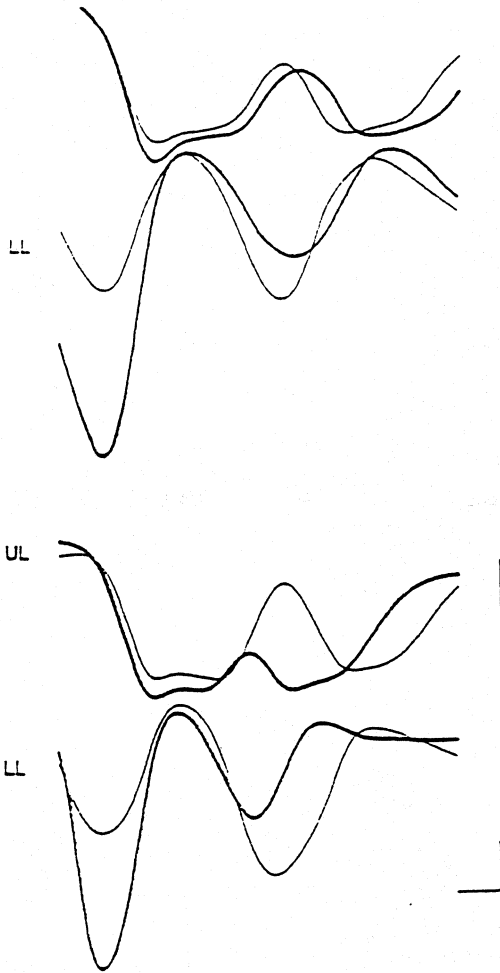


Fig. 8. Single trials examples illustrating the differential movement timing changes accompanying early and late load offsets in the LNF condition. Thin line represents the control (no load) movement, the thick line represents the perturbed movement. In the top panel, load removal occurred relatively early prior to P2 muscle onset (150 ms); in the bottom panel, load offset occurred relatively late prior to P2 muscle onset (20 ms). For the early load offset (top) the upper and lower lip movements are delayed relative to the control trial. In contrast, the later load offset (bottom) appears to result in an earlier or phase-advanced onset of upper lip and lower lip movement. Vertical calibrations reflect 2 mm for the UL and LL, respectively; horizontal calibration is 50 ms

curves in Fig. 7 (top), upper lip muscle adjustments did not parallel the lower lip adjustments and appear to compensate for the maintained lower lip increase following load removal.

The interburst interval was also analyzed in relation to load offset. Presented in Fig. 7 (bottom) are the mean changes in P1-P2 timing for the five 50 ms load offset intervals. Since the UL and LL muscle timing changes were similar, only the interburst timing for the LL muscle (OOI) is presented. As shown, the time between EMG onsets is signifi-

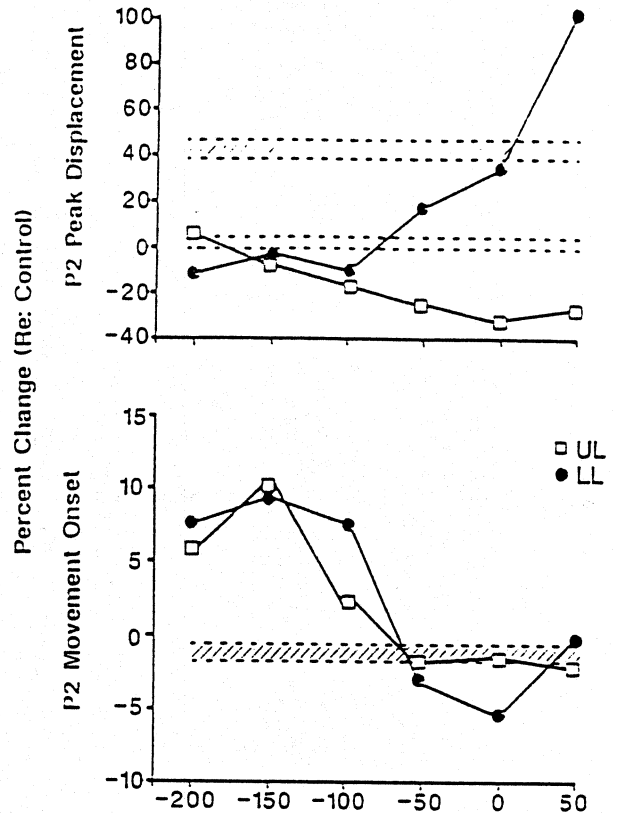


Fig. 9. P2 peak displacement (top) and movement onset (bottom) changes for the upper and lower lips (UL, LL) as a function of load offset (in ms) for the LNF condition. Responses were pooled and averaged as described in the previous figure (Fig. 7). Stippled areas reflect the group average (± 1 S.E.) for the LN condition; 0% reflects the control condition; diagonal stipple reflects the LL range, vertical stipple reflects the UL average. Horizontal axis is load offset time (ms) relative to the time of P2 OOI onset. The different upper lip/lower lip displacement changes can be seen in the top part of the figure. The lower lip displacement changes increase with later load offsets; however, the upper lip does not follow the same pattern. Rather, the upper lip changes appear to rely heavily on the presence of the lower lip load whereas the lower lip changes appear more predictive after approximately 100 ms before P2 OOI onset. In contrast, movement onset timing is adjusted in a similar manner for the upper and lower lip movements

cantly longer ($P < 0.01$) than the control (control = 0%) for early load offsets (90 ms and earlier prior to P2 onset) and shortens as load removal occurs closer to the second movement. In general, progressively later load offsets result in interburst timing similar to that found for the LN condition (LN mean = -5%). Apparently, if the load is still present approximately 50 ms prior to EMG onset, the timing of the second movement is set and proceeds as if the load had remained on.

The differential load offset timing patterns and their effect on the resulting kinematics can be seen

qualitatively in Fig. 8. In the two single trial load/control comparisons, it can be seen that a load removed at approximately 150 ms before P2 EMG onset (Fig. 8, top) results in a delay in the movement onset for both UL and LL movements. Conversely, late load offset (Fig. 8, bottom; 20 ms before P2 EMG onset) results in a shorter movement onset for both upper and lower lip movements. Figure 9 presents the UL and LL movement displacement and movement onset changes for the different load offset intervals for all subjects. There are obvious UL/LL differences seen in Fig. 9 (top). Indeed, while UL movements show increased reduction with later load offsets, the LL movement for late load offsets increase and actually overshoot the LN range substantially. This is in contrast to the EMG area changes for the LL muscle previously presented (Fig. 7, top) which never reached the LN range, even for the loads removed 40 ms after P2 EMG onset. The most plausible explanation is that the release from the load coupled with the higher levels of EMG activity associated with late load offsets combined to produce the overshoot. In contrast, the UL changes to load removal were always reduced from the LN condition. As shown in Fig. 9 (top), the UL displacement changes never approached the LN condition mean except for the very earliest load offset times. In comparison to the differences in the UL and LL displacement changes presented in Fig. 9 (top), the UL and LL movement onset changes (Fig. 9, bottom) are similar to the EMG timing results shown for the lower lip muscle (OOI; Fig. 7, bottom).

As noted previously, EMG activity from a jaw closing muscle (medial pterygoid) was also obtained in one subject. The jaw muscle activity changes were similar to those reported for the lower lip muscle. Specifically, EMG area changes were observed for both the LN and LNF conditions; for the constant load, the jaw muscle increased 25% in contrast to only 13% for the short load resulting in a significant reduction ($P < 0.01$). Interburst timing was also found to change with the load; however, the change was unidirectional. Removal of the load resulted in a statistically significant increase in the interburst interval ($P < 0.01$) for early load offsets; no significant EMG timing change was found for the constant load condition.

Discussion

The kinematic and EMG changes observed in response to lower lip load manipulation indicate that each serial multiarticulate movement comprising a speech movement sequence is individually modifi-

able after the initiation of the sequence. While it has previously been suggested that multiarticulate speech movements involve time-dependent sensorimotor mechanisms (Abbs and Gracco 1984; Gracco and Abbs 1985) the present findings suggest that such time-varying mechanisms underlie the programming of each movement in a sequence. As such, it appears that the detailed muscle contractions and resulting kinematics rely on sensorimotor mechanisms to implement the individual serial adjustments. Further, EMG magnitude scaling and interburst timing adjustments for the individual multiarticulate movements are specified at different times prior to movement execution. Finally, the present results suggest that timing and magnitude adjustments may rely on different nervous system regions for their implementation. These conclusions will be discussed below.

Speech motor programming

The characteristics of speech movements can be considered within the construct of a motor program. Previous results suggest that single multiarticulate speech movements involve the assembly of flexible task-specific, functionally-related motor commands adjusted for peripheral conditions (see Abbs et al. 1984; Gracco and Abbs 1985; Kelso et al. 1984). An additional component of this motor process involves a central patterning of motor commands for all synergistic muscles facilitating the timing and subsequent coordination of the multiple degrees of freedom (Gracco and Abbs 1986; Gracco 1988). Speech motor programming can be thought of as a real-time multi-staged process involving the activation of relevant muscles, inherent specification of their relative timing, and the sensory-mediated scaling of contraction parameters (e.g., amplitude, duration, and rise time) based on peripheral conditions and performance objectives. Similar conceptualizations have been proposed for most purposive motor behaviors (Bernstein 1967; Schmidt et al. 1979; Schmidt 1982; Turvey 1977) focusing primarily on central mechanisms while acknowledging the influence of sensory interactions (however, see Bernstein 1967; Saltzman 1979). The present results and those previously reported for speech and other skilled motor behaviors (Gentner 1987; Gracco and Abbs 1985; Gracco and Abbs 1986; Gracco and Abbs 1988) suggest that motor programming involves a blend of central and peripheral influences with the peripheral influences continually available to modify motor performance. In contrast to the suggestion by Schmidt et al. (1979) that peripheral influences do not seem to be involved in the selection of new

responses, results from Georgopoulos et al. (1981) and Soechting and Lacquaniti (1983) indicate that peripheral sensory influences can assist in the correction as well as selection of new responses. The multiple stages and sensory-mediated nature of speech motor programming would allow for intervention and modification at various levels providing the flexibility required for speech movement coordination (see Gentner 1987 for results from typing and other skilled motor behaviors).

Previous investigations attempting to address the programming of serial speech movements, have suggested that components of serial or sequential actions are prepared entirely prior to execution (Kozhevnikov and Chistovich 1965; Lashley 1951; MacKay 1970; Schonle et al. 1986). To a large extent these studies have utilized as a dependent variable the time required to initiate a motor task, the reaction time (RT); the detailed EMG or movement characteristics in these studies were not analyzed directly. It should also be noted that programming has been used in a more restricted sense in many of the previous studies. While it is clear that RT required for response initiation may be influenced by the complexity (Sternberg et al. 1978) or nature of the response (Schonle et al. 1986) the present study suggests that specifying the magnitude and timing of individual speech motor actions is not necessarily how that initiation time is utilized. Sets of sequential speech movements may be planned (i.e., generally selected) in terms of an entire goal-directed action; however, the magnitude, and to a lesser extent, the timing of each serial element is specified on a movement-to-movement basis.

Similarly, for movements of the upper limb, it has been suggested that each element of a novel sequential action involves the serial execution of independent motor programs (Benecke et al. 1986). In the present study, the change in timing between the first and second bursts of EMG activity and the upper lip adjustments for the opening movement prior to the second closing movement (Fig. 4) supports the interpretation that the elements of the movement sequence were not programmed as a unit. Further, the change in timing of the second movement has a functional interpretation consistent with the notion of independent actions. The earlier onset of the second closing movement with the continuous load can be interpreted as a means to reduce the extent of oral opening. That is, the earlier onset of muscle actions for the closing movement effectively limits the amount of oral opening (due to the inferiorly-directed opening force) and the subsequent extent of oral closing. Similarly, when the load is removed, the resulting motor delay permits a readjustment to the

altered peripheral conditions to minimize overshoot. It is interesting to note that the time when load removal results in the largest "reprogramming" delay (100–200 ms before P2 EMG onset) is the time when peripheral conditions are rapidly changing due to the oral opening prior to the closing movements. Sensory information during this time period (early stage of oral opening) could be used to predictively scale the upcoming motor commands for the subsequent closing movements (Gracco and Abbs 1985; Gracco 1987). Finally, the differential timing changes with load removal suggest that relative timing of contiguous speech movements may not be an invariant feature as has been suggested for gait (Carter and Shapiro 1984).

While it is apparent that multi-element motor sequences are not programmed as a whole, the present data do suggest that some portion of the overall speech motor sequence may be specified prior to the first movement. This suggestion is supported by the observation that EMG magnitudes for the second movement were slightly increased even if the load was removed well in advance of that movement (> 150 ms). Since early load offset is associated with an early load onset for the first agonist burst, the small residual increase in EMG magnitude could reflect an adjustment in overall excitability during an early stage in the motor implementation process; specifically, prior to and during the labial posturing for "p" preceding the successive opening and closing movements. To this point, Bernstein (1967) suggested that the central nervous system utilizes a preliminary "tuning" of all participating sensory and motor elements in the intended motor program in advance of the actual movements. Further support for an overall presetting of excitability comes from studies utilizing reflex excitation (e.g., Gottlieb et al. 1970; Kots 1977) to evaluate changes in motoneuron pool excitability occurring in advance of a voluntary movement. In the present experiment, the early presence of the load may have increased the excitability of the sensorimotor system, yielding a general increase in all subsequent motor commands; a modification not susceptible to later sensorimotor readjustment. In general, these particular findings may indicate that the overall responsiveness of the sensorimotor system may be grossly specified well in advance of the detailed programming and subsequent execution of each movement in the sequence.

Time-varying temporal and magnitude specifications

In analyzing the influence of load removal it was apparent that the time course of EMG magnitude

and timing adjustments was different. Specifically, the timing of the subsequent EMG onset appeared to be set by approximately 50 ms prior to EMG onset while magnitude adjustments were manifest for loads removed as much as 70–90 ms later (20–40 ms post-EMG onset). The apparent gating of sensory influences on timing specification may reflect the minimum latency required for afferent information to modify EMG timing. Further, sequential movement timing apparently reflects a more predictive process less dependent on peripheral sensory information than the specification of magnitude characteristics. The fact that magnitude adjustments are still possible at least 30 ms after EMG onset, apparently reflects established or pre-set sensorimotor contingencies (cf. Abbs et al. 1984).

Of note also is the difference between the time-varying compensatory capabilities of the upper and lower lip muscles associated with load removal. For late load removals, it appears that the lower lip muscle was operating in a more predictive manner than the upper lip muscles. That is, removal of the load at or after EMG onset resulted in OOI area values well above control. In contrast, EMG area values for the upper lip muscles were similar to the control condition. Apparently, upper lip EMG increases can be largely generated by the increased lower lip afferent input. Conversely, the lower lip EMG increases, being substantially larger to compensate for the load, require an additional input to facilitate the increased afferent input from the load. The differential upper lip, lower lip responses augment those reported previously for discrete multiarticulate speech movements (Gracco and Abbs 1985). Indeed, the present study suggests that sequential movement control is not fundamentally different from the control previously suggested for discrete multiarticulate actions.

Possible neural correlates

The different influence of the load conditions on the specification of sequential movement timing and magnitude suggests that these two sets of parameters may reflect different levels of the motor control hierarchy, and perhaps different neural mechanisms. Results from the present study indicate that the timing between serial speech motor action is established in advance of the final magnitude adjustments. Recent findings on readiness potential (Bereitschaftspotential-BP) changes overlying the frontal cortex during sequential motor tasks have been interpreted to indicate that the supplementary motor area (SMA) may be involved in the triggering process

for initial and subsequent timing of serial elements (Deecke et al. 1985). The BP changes, presumed to overlie SMA, precede the slow potential changes overlying other areas of cortex and are temporally related to the onset of each serial action. These observations are consistent with regional cerebral blood flow studies indicating parallel SMA changes for both "internal programming" and execution of a sequence of finger movements (Roland et al. 1980). For speech, it has been shown that the amplitude of the readiness potential is maximal over the SMA (Grozinger et al. 1979). Given clinical findings demonstrating speech production deficits following SMA lesions (Arseni and Boetz 1961; Caplan and Zervas 1978; Damasio and Van Hoesen 1980; Masdeu et al. 1978) this cortical area, with basal ganglia influence via VL thalamus (Schell and Strick 1984), is a plausible system involved in the control of sequential speech movement timing.

Because the magnitude adjustments for serial speech motor actions are more available to change throughout the entire movement sequence, other centers are likely to be implicated. Based on the multiple neocortical actions apparently involved in orofacial motor control (Muakkassa and Strick 1978; Schell and Strick 1984) it has been suggested that spatial adjustments in orofacial movements reflect at least two neural systems (Gracco and Abbs 1987). Specifically, well before movement onset the parameterization of the individual movements may involve the classic programming centers (basal ganglia-SMA, cerebellar-premotor). By contrast, later adjustments may involve more direct "transcortical" influences which have been preset by the programming centers (cf. Gracco and Abbs 1987). From this perspective, the present data reflect the access to programming centers prior to movement onset which give way to on-line execution processes immediately preceding each sequential movement.

Over the years, the concept of a motor program has broadened from a set of stored stereotyped commands to a more elaborate process involving multiple hierarchies of specification with differing levels of complexity (cf. Brooks 1979; Keele 1981; MacKay 1985; Saltzman 1986; Schmidt 1982). The present results provide further evidence for a multiplicity of levels underlying the programming of sequential multiarticulate speech movements. While serial speech movements apparently require a grossly-specified activation level and general timing relations prior to movement onset, the detailed magnitude and temporal adjustments for each sequential element can be differentially influenced by sensorimotor actions. An interpretation of the present study is that sequential multiarticulate speech

movements can be continually influenced by peripheral conditions and adjusted on a movement-to-movement basis by the current and predicted state of the effectors. Such movement-to-movement adjustments suggest that motor programs for speech may be more appropriately considered to reflect certain generalized motor actions (e.g., opening, closing, protrusion, retraction) rather than individual words, syllables, or other linguistic categories (see also Browman and Goldstein 1986). In this same vein, it is reasonable to suggest that most functional motor behaviors involve the continual assembly of basic motor actions, reflecting higher level goals and task performance objectives, adjusted for peripheral conditions and differing biophysical properties, to produce a complex of coordinated movement patterns.

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