

Dynamic Control of the Perioral System During Speech: Kinematic Analyses of Autogenic and Nonautogenic Sensorimotor Processes

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SUMMARY AND CONCLUSIONS

1. Afferent contributions to the motor control of speech were evaluated by applying unanticipated loads to the lower lip during the combined upper lip-lower lip gesture associated with the oral closing movements for a "b" sound. Loads were introduced randomly in ~15% of the trials to minimize subject anticipation or adaptation. A total of 490 load trials (in five naive subjects) were distributed within a restricted interval (100 ms) centered on the initiation of agonist muscle contraction associated with the lip-closing movements. Kinematic adjustments of the upper and lower lips to these perturbations were examined in detail.

2. In all subjects, load-induced changes in upper and lower lip displacement, movement time, and closing velocity were statistically significant and observed the first time a perturbation was introduced. Load timing variations within the target interval resulted in systematic changes in the site of the compensatory adjustments (upper versus lower lip) and in the magnitude of the kinematic responses. These kinematic changes appeared to reflect the dynamic nature of underlying control processes and clearly contrasted the different response characteristics of autogenic (lower lip) and nonautogenic (upper lip) compensatory actions.

3. Although both upper and lower lip adjustments contributed to perturbation compensations, autogenic responses were found to predominate when loads occurred 20–55 ms before muscle activation. For these early loads, autogenic responses provided

~75% of the total compensation. For later loads, when the evolving speech motor action was more time constrained, nonautogenic (open-loop) compensations predominated, providing ~65% of the total compensation.

4. The variations in upper and lower lip compensatory response magnitude did not parallel the time course of facial muscle activation. Lower lip kinematic adjustments were reduced 10–15 ms prior to the onset of agonist muscle activation, whereas upper lip adjustments increased in magnitude 10–20 ms after agonist onset. Apparently the dynamic modulation of these responses is controlled independently from facial motoneuron excitation, possibly involving sensorimotor processing via supranuclear centers.

5. Overall the compensatory movement displacements were highly related to the magnitude of the perturbation displacement, especially for loads introduced prior to agonist muscle onset, reflecting a well-calibrated readjustment. Responses to later loads were less consistently related to perturbation displacement.

6. Although compensatory displacements were manifest in a calibrated manner, adjustments in movement velocity and movement time were more variable and appeared to be subordinate to displacement adjustments. In one of the subjects movement velocity and movement time was strikingly different from those of the other subjects. These data were interpreted to suggest that even in a motor task such as speech, where some temporal constraints are manifest, the nervous system control process has flexibility in disassociating these kinematic variables.

7. These data suggest that afferent information from the perioral region is used in multiple ways in control of lip movements for speech. Prior to agonist muscle activation, based on the well-calibrated responses, afferent information is seemingly used to specify and update control parameters as part of what has been termed *motor programming*. Once motor execution is under way, afferent input is used to shape the evolving motor output, primarily via nonautogenic adjustments, to ensure achievement of multimovement goals.

INTRODUCTION

Recent experiments have implicated sensorimotor mechanisms in the moment-to-moment control and coordination of speech movements (3, 17, 18, 32). These studies have demonstrated the operation of robust, task-dependent, and automatic compensatory responses to unanticipated perturbations applied prior to or during a speech movement. Compensations have been observed consistently the first time a load is introduced, and perturbations do not disrupt the intended speech output. Compensatory adjustments observed in these studies appear to be autogenic as well as nonautogenic. For example, when jaw movement is perturbed for a jaw-lip movement task, a significant component of the compensation is a nonautogenic movement response of the lips (17). Comparable nonautogenic sensorimotor actions have been demonstrated during rapid postural adjustments (35, 37, 38), eye-head movements (6, 36), wrist-thumb interactions (46), and thumb-finger actions (10, 11). These nonautogenic sensorimotor actions may reflect an important mechanism of complex movement coordination.

In an earlier paper (3) we reported that the sensorimotor responses to lower lip loads, introduced prior to or during a coordinated upper lip-lower lip movement, were manifest in the multiple synergistic muscles of the upper and lower lips at a range of latencies. In general, the compensatory responses appeared to vary as a function of the timing of the perturbation relative to the onset of lower lip muscle activation. These changes may be comparable to compensatory response variations observed when the lower limbs are

perturbed during different phases of the step cycle (20, 21) or when torque pulses are applied to the human arm at various points during maximally rapid flexion movements (15). Such observations suggest dynamic changes in sensorimotor or reflex actions based on the time course of the evolving motor act. In this vein, one purpose of the present study was to examine upper and lower lip kinematic compensatory responses associated with variations in the timing of lower lip perturbations. Additionally, we wished to refine observations made in that earlier paper regarding the apparent sensorimotor differences between upper and lower lip compensatory responses to lower lip perturbation.

Results from this study indicate that the compensatory response kinematics change systematically in magnitude and locus (upper versus lower lip) with the time of perturbation relative to the evolving movement. These time-dependent kinematic changes to lower lip perturbation also quantitatively distinguish the autogenic adjustments of the perturbed lower lip from the nonautogenic or feedforward adjustments of the unperturbed upper lip.

METHODS

Subjects

Subjects consisted of five adult females between the ages of 25 and 35 years of age. All subjects reported negative neurological and developmental histories and exhibited no obvious speech difficulties as judged by the experimenter. All subjects likewise were naive as to the objectives of the experiment and unaware of techniques and procedures in motor control studies.

Lower lip perturbations

Unanticipated perturbations were applied to the lower lip in an inferior direction, using a brushless DC torque motor (Aeroflex No. TQ34W-12). Details regarding the operational characteristics of the torque motor were described previously (3). Rotation of the torque motor sector arm was transmitted to the lower lip via a stainless steel wire and a single low-friction lever. The torque motor control circuits were designed to operate under force feedback control and to follow speech movements at tracking loads < 5 g. With these small tracking forces, subjects report that they are able to produce normal speech movements without any sensation of movement restriction.

Signals recorded

A number of signals were simultaneously recorded. These included 1) displacement of the upper lip and lower lip (inferior-superior dimension) with the displacement signal provided by the rotational variable differential transformer (RVDT; Pickering) coupled to the brushless DC torque motor (lower lip) and a cantilever beam instrumented with a strain gauge transducer (cf. Ref. 5) firmly attached to a head stabilizing device (upper lip); 2) force output from the torque motor; 3) EMG from four perioral muscles, with hooked-wire electrodes; and 4) a control signal that was used to specify both the magnitude of the force perturbation as well as the force rise time. The bandwidth of the RVDT and the strain gauge transducer (DC to at least 40 Hz) exceed the range of normal speech movements. All EMG signals were preamplified with a frequency range of 22 Hz to 20 kHz, a common mode rejection ratio of 110 dB, and an input impedance of 1,000 M Ω . Additional amplification was obtained from Honeywell Accudata 135 amplifiers with filter settings of 50 Hz high pass and 2.5 kHz low pass. All signals were digitized on-line using a DEC PDP-11/44 lab computer. Myoelectric activity was digitized at 5,000 samples/s, whereas movement and force signals were digitized at 700 samples/s.

Movement task

As previously mentioned, subjects were not aware of the purpose of the study and were instructed that this was a reaction time (RT) experiment. The subjects' task consisted of sustaining the vowel "ah," and on hearing a tone (1,000 Hz, 250 ms duration) to close their lips as rapidly as possible and generate a "b" sound. Once the sound was produced they were to resume producing the vowel and respond again when the tone was heard. Effectively subjects were producing rapid lip closure from a static posture. The only demands placed on the subject regarding the task was that the "b" be generated in a manner that was unambiguous to a human listener. From an ecological perspective, the exact movements of the lips are subordinate to the acoustical goals of this natural, well-learned speech motor task.

Perturbation characteristics

Controlled loads of 250 ms duration with different magnitudes and rise times were used to produce a range of perturbation displacements and velocities. Two discrete force rise times (5 and 15 ms) and two levels of force magnitude (35 and 55 g) were used. These force magnitude-rise time combinations resulted in displacements and velocities within the range of normal lip movements for speech (cf. Refs. 28, 44). By varying the force magnitude it was possible to introduce large-

magnitude errors even after the initiation of muscle contraction. In our previous study a single force magnitude was used and perturbation displacement varied only as a function of lower lip stiffness (i.e., the contraction level of orbicularis oris inferior) at the time of load onset.

Introduction and control of perturbations

All aspects of the data acquisition procedure were under computer control, with interactive manipulation by the experimenter. The onset of the auditory stimulus, controlled by the experimenter, served as a trigger for a chain of programmed events. Each stimulus-tone presentation triggered the PDP-11/44 to access a stimulus table that engaged one of the following conditions: 1) initialize the data acquisition program, 2) initialize the data acquisition program and deliver the perturbation to the subject, or 3) skip to the next entry in the table. The initialization of the data acquisition program digitized the physiological signals of interest for a 500-ms period beginning at tone onset. If a perturbation entry was encountered, the data acquisition proceeded (condition 2) and a shaped pulse was sent in parallel to the torque motor control circuit. A manually operated key-in on a computer terminal provided a means to delay the onset of the perturbation relative to the onset of the auditory tone. Perturbations were delivered randomly at an average frequency of 15% (i.e., 15 perturbations/100 trials). The low percentage of perturbations was necessary due to concerns regarding adaptation/anticipation (3). Each perturbed (experimental) trial was digitized along with the immediately preceding control trial. These control-experimental pairs were used in statistical analyses of perturbation-related changes. The signals from all trials were recorded on FM tape.

Loads were applied prior to and during the initial phases of the major agonistic muscle contraction associated with the two lip movements under investigation. Electromyographic activity from a muscle involved in the lower lip elevation movement (orbicularis oris inferior) was monitored on an oscilloscope by the experimenter. By observing the muscle activity onset relative to the onset of the stimulus tone (RT), it was possible, via the computer key-in delay, to deliver perturbations within a narrow range relative to activation of this muscle. Specifically, the target interval for the introduction of these loads was the 100-ms window centered on the onset of orbicularis oris activation; this target interval for the lower lip loads is shown in Fig. 1 for the speech task "aba." Approximately 125 responses were obtained from each subject, of which ~100 fell within the 100-ms target interval. Subjects were not informed of the possibility that speech movements might be perturbed.

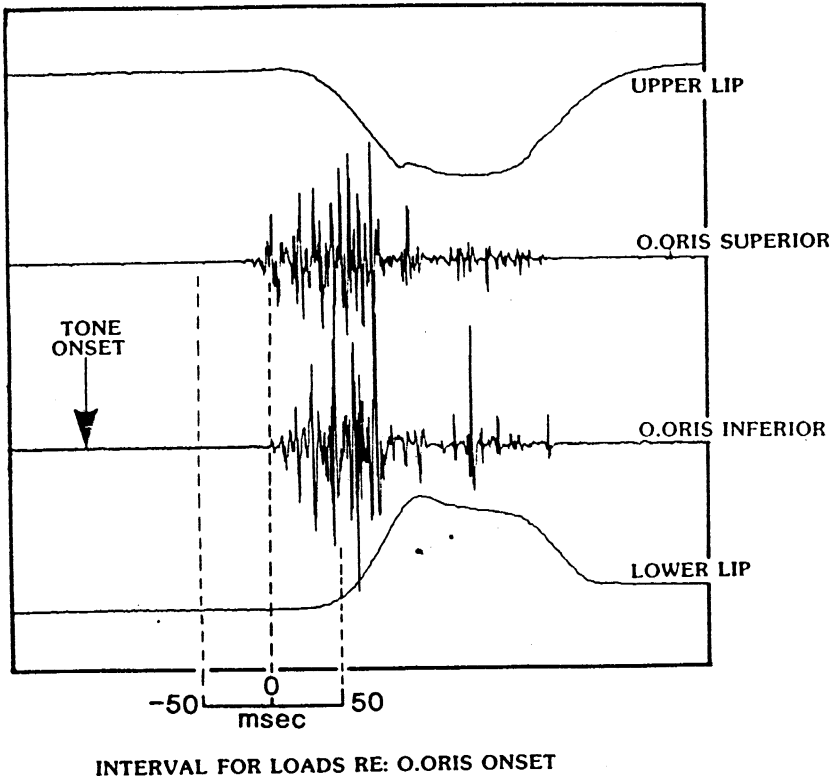


FIG. 1. Target interval for the introduction of perturbations. Load onset times are relative to the onset of the voluntary EMG activity recorded from the orbicularis oris inferior (OOI) muscle.

Data analysis

A total of 490 control-experimental trial pairs were obtained from the five subjects. Following the on-line data acquisition, each perturbed and control record was individually viewed on a DEC-VT100 Retrographics terminal. As shown in Fig. 2, specific events were labeled and marked for subsequent analysis. Based on these event markers, computer programs were used to provide the following measures: 1) time of load onset relative to initiation of contraction in the lower lip elevation agonist muscle (orbicularis oris inferior); 2) lower lip displacement caused by the perturbation as well as associated perturbation velocity; 3) displacement and instantaneous peak velocity of both upper and lower lip movements for the oral closure for "b" and associated duration of those movements. Peak movement displacements for each lip were calculated as the difference between the position of each lip immediately prior to movement onset and the maximum lip positions at closure. Movement time was measured as the time from movement onset to maximum displacement. Instantaneous peak velocity was obtained by software differentiation of the digitally filtered

(20 Hz low pass) movement signals. By obtaining these measures from both the control and experimental trials, it was possible to evaluate the kinematic characteristics of the compensatory movements in relation to variations in perturbation displacement and timing. Comparable analyses were conducted on the EMG signals (e.g., magnitude of change and latencies) (V. L. Gracco and J. H. Abbs, unpublished observations).

Statistical procedures

The experimental and control responses were evaluated statistically to determine 1) the presence of significant control-loaded trial differences with analysis of variance (41) and paired comparison statistical tests and 2) specific relationships between the dependent variables of interest (e.g., compensatory magnitude) and variations of an independent variable (e.g., perturbation displacement) with correlational (Pearson product moment) analyses. The group data were analyzed with a one-way analysis of variance. Post hoc testing was undertaken with the least-significant difference test (42) to control for comparison-wise error. The acceptable alpha level for all statistical procedures was

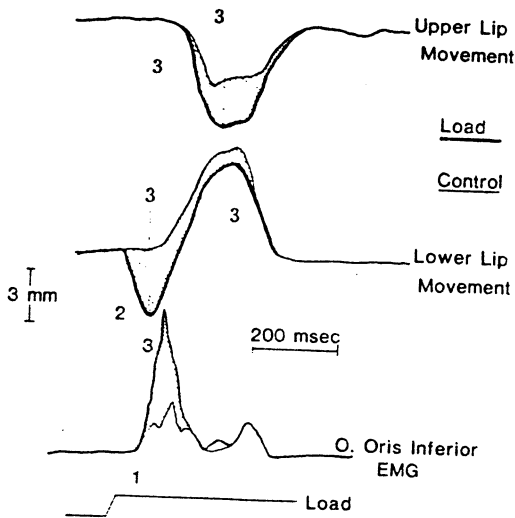


FIG. 2. Illustration of the events used to derive the measured variables. Load onset time is the interval from the onset of the load to the onset of the EMG associated with the voluntary responses (1). Perturbation displacement is measured from the onset of the lower lip displacement due to the load (2) to the maximum displacement created by the load (3). Movement displacement (control and perturbed) is taken from earliest indication of upper lip depression (3) or lower lip elevation (3) to the maximum closing displacement (3).

set at $P < 0.05$. For data from individual subjects, paired comparisons consisting of individual t tests were used to evaluate differences between the control and experimental measures (41).

RESULTS

A total of 490 perturbations were introduced in the target interval for the five subjects. As in the previous study (3), compensations were observed the first time a lower lip load was introduced and there were no trials in which the perturbation disrupted the successful achievement of the speech task. Similarly, compensatory response latencies fell within the range reported in the previous study (i.e., 25–80 ms). Analyses of the kinematic adjustments reflected the operation of multiple sensorimotor processes in the control of these lip movements for speech. Specifically, as illustrated below, variations in the timing of the perturbations resulted in systematic changes in the kinematic compensatory patterns that in turn differed for the upper and lower lips.

Overall kinematic changes

Figure 3 shows the mean peak upper and lower lip displacement for the loaded and control conditions for the five subjects. Paired comparisons revealed statistically significant increases in both upper and lower lip displacement ($P < 0.001$) for each of the five subjects. Similarly, upper and lower lip closure velocity and movement time with load also were increased significantly ($P < 0.001$). To determine the kinematic adjustments that were critical to successful accomplishment of this two-movement task, the relative consistency of the displacement, velocity, and movement-time change associated with the perturbations was examined. These analyses thus provide some direct information on the kinematic variables the nervous system is attempting to control (cf. Ref. 1), i.e., the potentially invariant control parameters. Not surprisingly, given the importance of occluding the oral opening for successful generation of "b," displacement changes were most consistent. As will be shown, movement duration and velocity varied in a subordinate and more variable fashion to achieve the necessary displacements. Obviously, to accomplish a given displacement, the potential exists for covariable changes in movement velocity and movement time. These and other kinematic adjustments are apparent in the results that follow.

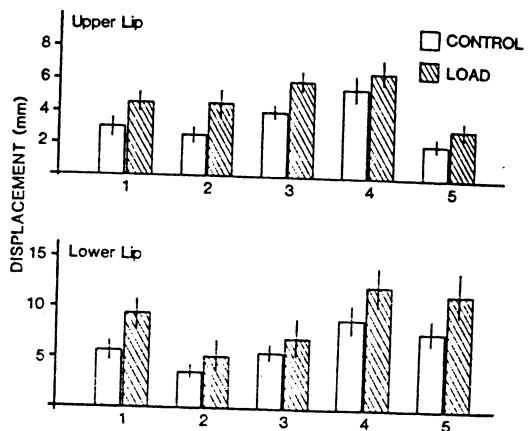


FIG. 3. Bar graph of mean upper lip and lower lip displacements at bilabial closure for the control and load responses for 5 subjects. Vertical line represents ± 1 SD. The numbers on the abscissa reflect individual subjects. The number of responses obtained for each subject (1–5) were 93, 102, 104, 93, and 98, respectively.

Time-varying characteristics

One of the major goals in this experiment was to examine the time-varying responses to load perturbation. Because the load onsets for individual subjects were not uniformly distributed in the 100-ms target interval (cf. Fig. 1), the data were pooled across subjects to allow for a more detailed examination of the time-dependent variations. Presented in Fig. 4 are the average perturbation displacement (load-induced input error; top trace) and the corresponding combined upper lip-lower lip compensation displacement (output compensation; bottom trace) for the 490 responses as a function of load onset time. These are mean values, each calculated from the subset of loads introduced within 10 adjacent nonoverlapping 10-ms intervals ranging from 55 ms pre-OOI activation to 45 ms post-OOI activation. The displacement compensation value (output) for each load trial was obtained by subtracting the peak displacement of the preceding control trial from the peak displacement of the loaded trial. This difference yielded the displacement compensation for each load-control pair. The dependence of the compensation displacement on the perturbation displacement is reflected by the parallel nature of the two curves in Fig. 4; the correlation of the mean perturbation displacement and mean compensation displacement for the 10 pairs of data points was positive and high ($r = 0.96$). Further, it is apparent from Fig. 4 that the perturbation displacement was not constant across the load onset time range. Provided in Table 1 are the correlation coefficients relating the perturbation and compensation displacements within each of the 10 load onset intervals. Overall, it appears that the movement compensation reflects a "cali-

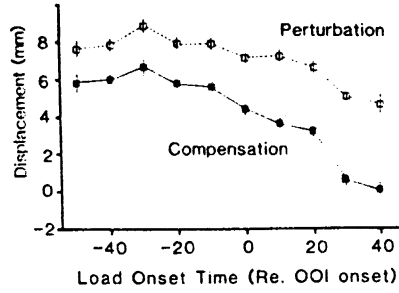


FIG. 4. Average perturbation displacement (top trace) and corresponding total (upper lip plus lower lip) compensatory displacement (bottom trace) as a function of load onset time. Vertical bars represent ± 1 SE. Data are pooled from all 5 subjects.

brated" response to the perturbation rather than merely a generalized overall increase. Moreover, the compensatory movement changes generally exhibit a stronger relationship to the perturbation in the intervals prior to EMG onset; for loads occurring at or after the onset of OOI EMG activity, the magnitude of the correlation between movement compensation and perturbation displacement is reduced.

To evaluate these time-varying responses as they related to the induced error, the ratio of compensatory displacement (X_c ; output) to perturbation displacement (X_p ; input) or "system gain" (X_c/X_p) was calculated for each load trial. This ratio provides a normalized measure of compensation relative to the magnitude of the displacement error resulting from the load perturbation. That is, a larger magnitude error generally resulted in greater compensations. By referencing the compensatory movement changes to the magnitude of the perturbation error, intersubject differences were minimized. These ratios were then averaged for loads occurring

TABLE 1. Relationship between perturbation displacement and movement compensation at each load onset interval

Load Onset Time (re: OOI onset)	-50	-40	-30	-20	-10	0	10	20	30	40
r	0.74	0.66	0.75	0.55	0.74	0.38	0.51	0.40	0.46	0.47
n	27	19	48	57	75	65	57	60	50	32
P	<0.001	<0.01	<0.001	<0.001	<0.001	<0.01	<0.001	<0.01	<0.01	<0.01

Correlation coefficients relating the perturbation displacement (X_p) magnitude to the movement compensation (X_c) changes for each load onset time interval. Also shown are the number of comparisons and the P value for each load onset interval.

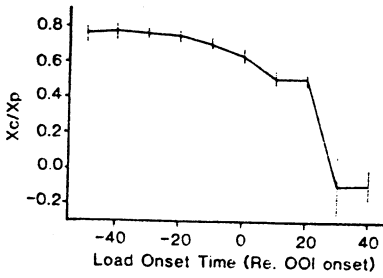


FIG. 5. Total system gain reflecting the ratio of combined (upper plus lower lip) compensatory displacement to the perturbation displacement error for each load onset time interval. Values represent means (± 1 SE) averaged over each 10-ms interval and centered on the interval.

within each of the 10 load onset intervals (as in Fig. 4). These output-input ratios, shown in Fig. 5, reflect the degree to which combined compensatory action of the upper and lower lips acted to overcome the displacement perturbation. A ratio of 1.0 reflects perfect com-

ensation, indicating the displacement perturbation was completely cancelled by the combined action of the upper and lower lips. As can be seen, although the system gain is high and relatively constant for early loads, it begins to drop off markedly at ~ 10 ms prior to agonist muscle onset. Overall, individual subjects show slightly higher or lower ratios across the 10 intervals; however, all subjects exhibited a reduction in total system compensation as the perturbation occurred later relative to the onset of voluntary muscle activation. As a matter of fact, for very late perturbations, system gain was negative indicating total compensatory displacement (upper plus lower lip) for the load trial was less than that of the control trial.

Upper lip-lower lip differences

Figure 6 shows upper and lower lip movements for multiple loaded trials for loads introduced ~ 45 ms (*B*) prior to OOI onset

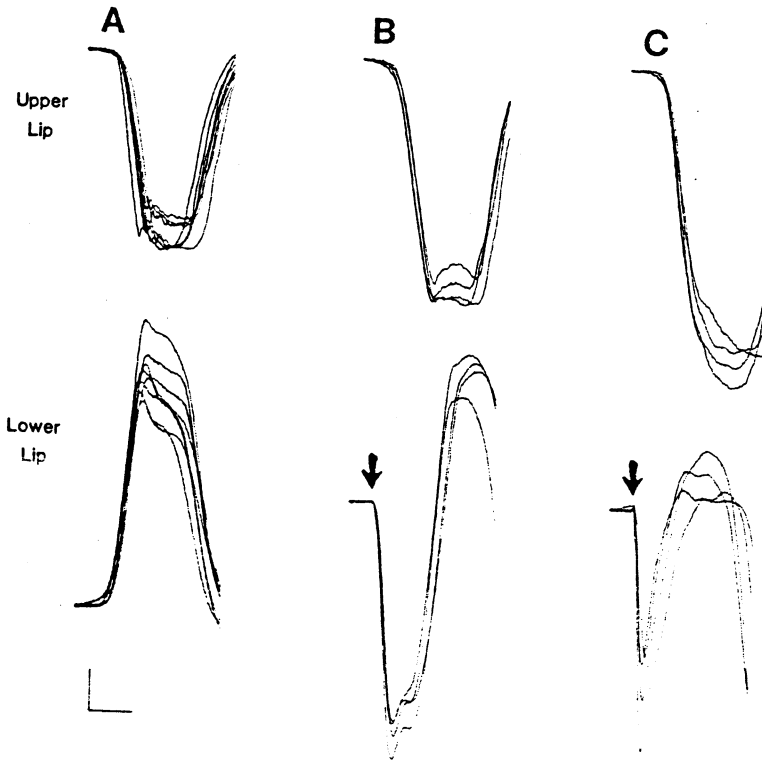


FIG. 6. Superimposed upper and lower lip movements contrasting responses to early vs. later occurring loads. *A*: corresponding control trials ($n = 8$). Early loads (45 ms prior to OOI onset) are presented in *B*; later loads (25 ms after OOI onset) are presented in *C*. Vertical calibration is 1 mm; horizontal calibration is 50 ms; arrow indicates load onset.

and 25 ms (*C*) after OOI onset. The corresponding control trials (*A*) are included for comparison. As is apparent, for early loads (*B*) that the relative amount of lower lip compensation is larger than the upper lip compensation, whereas for later loads (*C*) the relative amount of upper lip compensation is larger. This time-varying pattern of upper and lower lip adjustments was subjected to quantitative analyses, yielding a systematic pattern. Comparisons between the changes in displacement, velocity, and movement time for each lip in each experimental trial were calculated as a percentage of the value in the preceding control trial. This calculated value thus reflected the load-induced change in movement relative to the normal kinematics for each lip. As such, it was possible to determine the relative degree of upper versus lower lip adjustment to the load in comparable terms. For example, if a perturbation yields an increase of 6 mm in both upper and lower lip movement, this seemingly reflects equivalent upper and lower lip compensation. However, relative to normal (unperturbed) displacement of 6 and 10 mm for the upper and lower lips, this 6-mm compensation yields percent changes of 100 and 60%, respectively. Because significant intersubject variations in the absolute magnitude of upper and lower lip movements for speech have been demonstrated (31), normalizing compensatory changes in this manner also facilitated pooling of data across subjects. Utilizing this percentage change in lip displacement as a reflection of the output and the perturbation displacement as the input, a functional gain was calculated for each of the 490 load-control trials for both the upper and lower lip. Figure 7 shows these separate upper and lower lip gains pooled across subjects as a function of load onset time. These operationalized gains reflect a ratio of the percent change in the upper and lower lip displacement relative to the load-displacement magnitude. Positive values in these functions reflect increased movement for loaded trials (re control trials) and conversely. As shown, the lower lip provides greater relative compensation for loads introduced prior to muscle activation (10–50 ms pre-EMG onset) than the upper lip (9.4 versus 6.1; $P < 0.0001$). These gain functions also indicate that for early loads compensatory

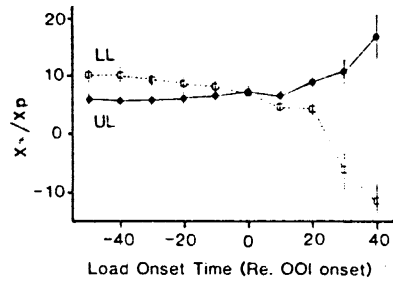


FIG. 7. Normalized upper and lower lip compensatory ratios (gain) for all subjects. Ratios represent the average (± 1 SE) compensatory change (expressed as a percent increase or decrease) in displacement divided by the magnitude of the perturbation displacement for each 10-ms load onset interval. Filled circles represent the upper lip (UL); unfilled squares represent the lower lip (LL).

adjustments yield proportional and relatively consistent increases in both upper and lower lip displacement. Later occurring perturbations (after OOI onset) result in a lower lip gain that is markedly reduced; by contrast, the upper lip contributes disproportionately as the load is introduced after the onset of muscle activation. For these later loads, the upper lip gain is greater than the lower lip gain (8.8 versus 2.8; $P < 0.0001$). These data document the independence of upper and lower lip compensations and augment our earlier interpretation that responses in the upper and lower lips represent two different sensorimotor actions.

The high correlation of perturbation displacement to movement compensation noted above indicates the importance of displacement as a control variable. It was also of interest to determine the manner in which these displacement compensations were achieved. For example, we wished to determine whether the load-induced displacement changes were accompanied primarily by concomitant velocity changes (possibly to preserve some intrinsic timing) or whether the larger displacements were accomplished solely by increased movement time. Overall the data indicate that increased displacement was accompanied by a combination of velocity and movement time changes; the relative degree of these velocity and movement time changes were influenced by the time of load onset. Figure 8 shows the average percent changes in movement time for the upper and lower lips pooled across

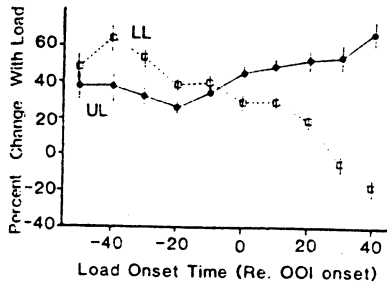


FIG. 8. The mean (± 1 SE) percent change with load in movement time for all subjects. Filled circles represent the upper lip (UL) closing movement time change; unfilled squares represent the lower lip (LL) closing movement time.

subjects and plotted as a function of load onset time. Inspection of these data indicate a constant increase in relative movement time during early occurring perturbations, with lower lip movement time changes consistently larger than those of the upper lip ($P < 0.001$). Similar to the time-varying changes in compensatory displacement, movement time changes also manifested an upper lip-lower lip crossover at ~ 10 ms prior to EMG onset, with upper lip movement times increasing more for later loads than those of the lower lip. These data thus suggest that the relative timing of the upper and lower lip movement is not preserved in the face of unanticipated perturbations. Parallel analyses of the relative timing difference between the upper and lower lip peak displacement, directly reflecting lip closure time, indicated that this relation likewise was modified with load perturbations for all subjects ($P < 0.0001$). In considering the movement time changes, it should be noted that a subset of the lower lip movement changes could be confounded because the later occurring loads (post-EMG onset) may obscure the actual movement onset. However, the upper lip movement duration changes to later loads (which are not similarly confounded) manifest a significantly greater increase in movement time than was observed for the earlier loads ($P < 0.001$), despite a somewhat different pattern in one of the subjects (unpublished observations).

The percentage of change in peak movement velocity also was examined as a function of load onset time. As can be seen in Fig. 9, the velocity changes also varied with load

onset timing. Lower lip velocity changes were greater than upper lip velocity changes for the earlier loads with a reversal of this relation for loads introduced approximately 10 ms before OOI onset. For the upper lip, peak velocity changes are relatively consistent and positive for loads occurring up to ~ 20 ms after OOI onset, followed by a constant decline. Not surprisingly, the upper lip movement times (Fig. 8) begin to increase at approximately the same time as the movement velocity changes are reduced. That is, although upper lip compensatory displacement increased for loads occurring 20–30 ms after lower lip muscle activation, the manner in which these compensations are achieved appears to be different from the compensations to earlier loads. These time-varying changes illustrate the differential action of upper and lower lip adjustments as well as the general trade-offs in movement time and velocity that are implemented to accomplish the necessary displacement. The variations in the kinematic adjustments with time of load onset were paralleled by electromyographic changes in the upper and lower lip muscles. Figure 10 illustrates EMG changes for orbicularis oris superior, depressor anguli oris (upper lip depressors), and orbicularis oris inferior (lower lip elevator). As is apparent, the lower lip EMG change is more pronounced for early loads, whereas the converse is true for the upper lip (V. L. Gracco and J. H. Abbs, unpublished observations).

Based on the time-varying kinematic response patterns from the total system (e.g., system gain) as well as the differential upper lip-lower lip changes in gain, movement time,

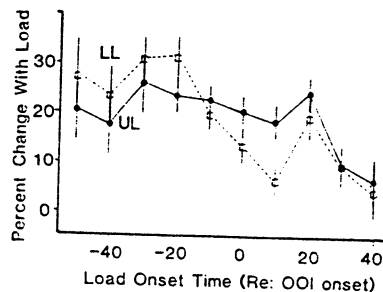


FIG. 9. The mean (± 1 SE) percent change in upper and lower lip closing velocity with load for all subjects. Upper lip (UL) and lower lip (LL) changes are indicated as Fig. 8.

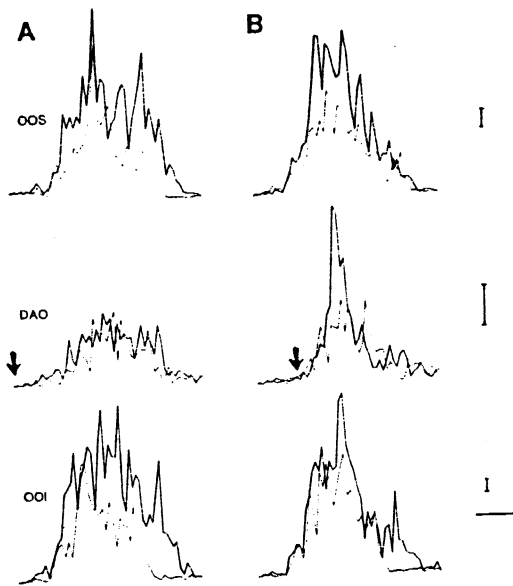


FIG. 10. Averaged ($n = 4$) EMG activity from 2 upper lip muscles orbicularis oris superior (OOS) and depressor anguli oris (DAO) and the major lower lip muscle orbicularis oris inferior (OOI) for (A) early (45 ms before OOI onset) and (B) later loads (20 ms after OOI onset). Vertical calibration is 100 mV; horizontal calibration is 50 ms; arrow indicates load onset.

and velocity, it appears that there may be several different sensorimotor actions involved in this lip movement control process. That is, responses to early loads (pre-EMG onset) appeared to reflect different compensatory patterns than responses to later loads

(post-EMG onset). Given these apparent differences, it was of interest to statistically compare the kinematic changes for early and late loads. As reflected in the above results, the kinematic changes appear to divide the total load onset time naturally into two intervals. The first interval (A) ranges from 55 to ~ 10 ms prior to orbicularis oris inferior muscle activation, whereas the later interval (B) ranges from approximately 10 ms pre- to 45 ms post-OOI onset. This division is a first approximation and the time-varying changes observed may realistically reflect three or more overlapping phases of control. Table 2 summarizes the changes in relative displacement gain, velocity, and movement time for these two intervals. As shown, all of these comparisons yield statistically significant interval A-interval B differences. Collectively, these results point to some functional time-varying changes, including a reduction in total system gain due to an apparent inability of the lower lip to compensate for loads introduced during interval B as compared with interval A. No comparable gain reduction is seen for the upper lip; indeed, upper lip contributions are increased from interval A to interval B. However, the way in which the upper lip achieves compensatory displacement appears different for intervals A and B. That is, during interval A the upper lip movement compensation is achieved with a greater reliance on a change in velocity, whereas during interval B the movement compensation is accomplished with a greater

TABLE 2. Comparison of interval A-interval B kinematic changes

Kinematic Parameters	Interval A	Interval B	Probability
Combined UL and LL gain (absolute)	0.752	0.422	<0.001
Gain (relative)			
UL gain	6.09	8.76	<0.0001
LL gain	9.36	2.8	<0.0001
Velocity			
UL	23%	18%	<0.05
LL	28%	12%	<0.001
Movement time			
UL	30%	50%	<0.001
LL	46%	20%	<0.001

Comparison of interval A and interval B kinematic changes with load. Combined upper lip (UL) and lower lip (LL) gain represents a ratio of compensatory displacement to the perturbation displacement. Separate upper lip and lower lip gains (normalized) represent a ratio of compensatory displacement (expressed as a percent change relative to the normal movement) to the perturbation displacement. These relative gain values reflect the average % change/mm of perturbation displacement. The upper lip and lower lip movement-velocity and movement-time changes reflect mean percent increases relative to the control trials.

reliance on increased movement time. Thus these comparisons further document the independence of autogenic (lower lip) and non-autogenic (upper lip) sensorimotor actions as well as illustrating their time-varying nature.

Intersubject variability

The data presented reflect the compensatory patterns for a group of five subjects. For many of the kinematic changes associated with the lower lip loads, differences among the five subjects were minimal. For example, the displacement gains as a function of load onset presented previously (Figs. 5 and 7) were very similar for all subjects. However, there were some intersubject differences worth noting, the most striking and interesting of which was the manner in which upper lip compensatory displacements were achieved by subject one, as compared with the other four subjects. The data from subject one and subject two were chosen to illustrate movement time and velocity trade-offs in response to the perturbation. Presented in Fig. 11 are these changes for these two subjects as a function of load onset time. As can be seen, these two subjects reflect different degrees of movement velocity change for later load-onset times. The top trace (subject one) shows increased movement velocity for later loads (see Fig. 9). In contrast, the second subject exhibits only minimal velocity increases for later loads, with the velocity of the compensatory movement less than that of the control values. The movement time changes for these two subjects are presented in the lower panel of Fig. 11. For the subject one the trend toward increased movement velocity accompanying the upper lip compensation was coupled with a relatively small constant increase in movement time. For subject two and other subjects in this study, the trend toward reduced movement velocity accompanying upper lip compensation for later loads was coupled with a large increase in movement time. From these different compensatory patterns in these two subjects it appears that velocity and movement time can be coadjusted in a manner that is subordinate to the achievement of compensatory displacement. The potential independence of the movement time, velocity, and displacement variables was also reflected in correlations between displacement and peak velocity. That is, the relationship between peak move-

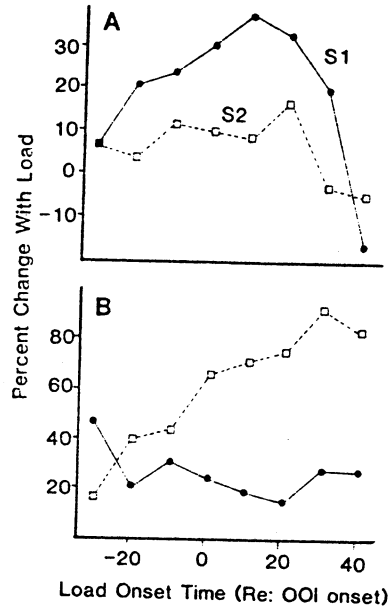


FIG. 11. Data from 2 subjects illustrating velocity (A) and movement time (B) changes in response to perturbation.

ment displacement and peak movement velocity in the control condition for all subjects was found to be high for both the upper and lower lip ($r = 0.894$ and $r = 0.98$, respectively). For the loaded condition the correlations for both upper and lower lip were reduced ($r = 0.78$ for both) indicating that the displacement-velocity relationship is mutable.

DISCUSSION

Based on these kinematic observations, there are notable differences in lower lip and upper lip movement compensations to lower lip loads. These differences, as suggested in a previous paper (3), reflect the independence of lower lip and upper lip responses and augment the interpretation that they reflect different sensorimotor actions. Specifically, in that earlier paper, we argued that responses in the lower lip to lower lip loads represented an autogenic action, whereas responses in the upper lip represented a nonautogenic or open-loop sensorimotor adjustment. The present data support such a distinction.

Regarding the functional significance of these two sensorimotor processes, it is useful to consider the larger behavior in which they operate. Lip movements for speech are com-

ponents of a complex multiple-movement action. Specifically, these movements must be executed in combination with other significant motor actions (e.g., lingual, respiratory, laryngeal, etc.) that are inherent to the total speech gesture. It has been known for several decades that relatively precise timing among these multiple movements is critical for intelligible speech. Lip movements for speech are thus generated under some finite time constraints. Similar temporal constraints exist for such diverse motor adjustments as postural reactions to destabilization and head-eye movements for rapidly changing targets. On the other hand, whereas the perturbations used in the present study yielded significant functional compensations (i.e., the speech goal was accomplished), movement velocity and movement time, obviously indicative of temporal control, appeared to covary, indicating that these variables were controlled in a manner subordinate to the control of movement displacement. Similarly, based on the reduced correlations between peak velocity and displacement in the load condition it appears that these kinematic variables can be controlled independently. Further, in a recent experiment using a similar perturbation paradigm on the lips of Parkinson subjects during speech, it was found that although these subjects were able to compensate for the induced perturbation, increased movement often was not accompanied by concomitant changes in peak movement velocity (27). In this same vein several of the observations from this study indicate that upper and lower lip movement time (or timing) was adjusted independently. Obviously there is some tolerance in the temporal patterning of the multiple movement constituents of this motor behavior. Similarly, even in the displacement domain, upper and lower lip adjustments did not fully compensate for the magnitude of the induced error.

This incomplete compensation is seemingly contradictory with the consistent observation in this and earlier studies (3, 26) that these lip perturbations do not disturb successful achievement of the intended speech goal. Several factors may account for this apparent paradox. First and most importantly, the degree of necessary accuracy for a speech task, such as this, is determined by the ecologically significant generation of an acoustic signal that is acceptable to a human listener.

Obviously, tight midline closure is not absolutely necessary to produce the necessary acoustic characteristics associated with an acceptable "aba." Given the relatively small midline lip area displaced by the paddle, it is possible that precisely the same degree of lip closure at the midline was not necessary. In fact, an acoustically appropriate "b" sound can be made even though the medial portion of the lips do not approximate fully.

Despite the temporal flexibility noted above, speech is a motor behavior with some temporal constraints. On this basis, it is possible to further interpret our observed differences between lower lip (autogenic) and upper lip (nonautogenic) compensatory responses. Previous work has indicated that autogenic responses are most effective when time is not a critical variable. Observations by Rothwell, Traub, and Marsden (40), for example, indicated that autogenic responses to thumb perturbations were effective only if sufficient time (300 ms) was permitted. Similarly, autogenic responses have been reported to be minimal or absent for perturbations of single joint movements executed under severe time constraints (14). In those more restricted single joint-movement tasks the possible sensorimotor actions were limited to autogenic adjustments, perhaps unnaturally (cf. Ref. 1). In contrast, a common finding in investigations of perturbed multiarticulate motor behaviors is the exclusive manifestation of nonautogenic sensorimotor actions (17, 18, 46) or, as in the present study, combined autogenic and nonautogenic sensorimotor actions (10, 11). For example, Folkins and Zimmermann (18) observed only open-loop or nonautogenic responses in response to lower lip perturbations; in contrast to the present results, no autogenic responses were observed. However, Folkins and Zimmermann (18) delivered most perturbations immediately prior to or during the lower lip movement. Because the onset of lip movement corresponds to a point ~25-35 ms after the onset of agonist muscle EMG. Folkins and Zimmermann's load onsets were very late (re load onset times in the present study). The absence of autogenic responses merely may reflect these load-timing factors. In this context, it is appealing to interpret the predominance of nonautogenic adjustments in time critical situations (as observed in the present study) as a general phenome-

non in natural multiarticulate movements. Specifically, when movements with multiple degrees of freedom are perturbed, both autogenic and nonautogenic sensorimotor actions may be used; however, nonautogenic or open-loop responses appear to predominate as time becomes a critical factor (e.g., for later loads). Because multiple degrees of movement freedom are manifest in most natural motor behaviors, the consequent availability of nonautogenic sensorimotor actions thus may increase the execution flexibility of time-critical motor actions. In general, this interpretation is consistent with previous analyses of motor control processes; it has been suggested repeatedly that autogenic adjustments are limited in their potential contributions to movement control, based primarily on temporal constraints (30, 39).

Time-dependent variations in sensorimotor actions of comparable functional significance have been reported for other motor behaviors. In the cat, stumbling corrective reactions (19) and compensatory responses to gait perturbation (20, 21) have been shown to vary in magnitude and sign (i.e., excitatory or inhibitory) with the phase of the locomotion cycle. The time-dependent response patterns observed in the present study suggest that analogous sensorimotor variations may operate in the dynamic control of human speech movements. However, it is important to note that the time-varying changes observed did not parallel changes in facial motoneuron excitability. That is, the compensatory responses in lower lip movement were substantially lower for loads introduced 20 ms after the onset of muscle activation than for loads introduced at the time of agonist muscle onset. The increase in upper lip compensatory displacement likewise was out of phase with the upper lip muscle activity. Similarly, the subtle, but complementary variations in compensatory movement velocity and movement time do not appear to be explainable by time-varying changes in lower motoneuron excitability. In this vein, the present observations do not merely reflect changes in the excitability of the motoneuron pool, as shown previously (7, 25, 29, 33). Rather, changes in system responsiveness appear to be influenced centrally. Similar suggestions have been made by Dufresne, Soechting, and Terzuolo (16).

Support for supranuclear influences on facial motoneurons comes from numerous sources. The most direct trigeminal afferent-

to-facial motoneuron connections (the perioral reflex; 12–18 ms) have been shown to be absent with the present perturbation paradigm (3, 26). Moreover, given the latencies observed in those previous studies (25–75 ms), it would appear that several suprabulbar pathways and centers (e.g., motor cortex, cerebellum) could be involved, but such suggestions can be made only tentatively. Inasmuch as the motoneurons innervating facial muscles receive monosynaptic input from motor cortex pyramidal cells (34), sensorimotor response characteristics may involve modulation via cortical circuits. For example, the reduced gain of the lower lip responses after EMG onset may reflect the inhibiting influence of central mechanisms that partially restrict afferent transmission (8, 9, 12, 24). It has been shown that dorsal column transmission from forepaw and hindlimb afferents is depressed prior to EMG onset for a voluntary movement, presumably via cortical influence (12, 24). Further, ascending transmission over numerous pathways has been shown to be influenced by the cerebral cortex (13, 45). Recent observations in primary somatosensory cortex (SI) in rats indicate that forepaw cutaneous stimuli are dynamically gated in their sensory transmission to SI during different phases of the locomotion cycle (8, 9). It remains to be shown that SI sensory gating also is influential in controlling motor cortex responsiveness to sensory input. However, Chapin and Woodward (8) did report that the general degree of such sensory gating was not only “temporally specific” but also varied with the motor task. In this respect, it is interesting to contrast the differential changes in upper and lower lip gain with later loads. Whereas the lower lip responsiveness is falling, the upper lip responsiveness is not, possibly reflecting differential modulation of these two sensorimotor processes via cortical influences. Such descending processes, if operating in the control of speech movements, also provide a possible explanation for the task-dependent sensorimotor variations observed previously (2, 32). For example, when a lower lip load is introduced during a speech action not requiring upper lip movements (“f”), compensatory responses are only observed in the lower lip (2). Seemingly functional sensorimotor adjustments can be gated in or out for various speech motor behaviors.

Overall, the findings of the present study augment recent reports of rapid modifications of aimed arm movements to changes in target location (22, 23, 43). The ability to modify movements throughout the motor act indicates, as suggested by Georgopoulos et al. (23), that movement control is a real-time continuous process (i.e., it is sensitive to inputs throughout the preexecution and movement time). Additionally, given that responses to early loads in the present study are characterized by a proportional increase in both upper and lower lip movement (cf. Figs. 5 and 7 and Table 1), these compensations appear to reflect a calibrated rescaling of the previously programmed speech movements. As such, responses to early loads may reflect the operation of a process whereby control parameters are specified and updated prior to the onset of motor execution, similar to a parameter estimation process (cf. Ref. 4). Such preexecution adjustments would appear to be an aspect of what some investigators have referred to as motor programming. In contrast, responses to later loads may reflect more time-critical adjustments of limited gain operating as part of the actual movement execution process. It is thus hypothesized that the sensorimotor actions observed in the present study include aspects of the programming and execution processes associated with the production of voluntary speech movements.

The responsiveness of the perioral system throughout the muscle action and movement

sequence also suggests that in normal circumstances the motor program parameters may be specified only generally. As the program is being executed, appropriately modulated afferent information is available to modify or shape the motor output in a corrective and predictive manner based on the evolving kinematics. Such on-line adjustments would allow for subtle trade-offs such as the intermovement, motor equivalence variations previously reported between the lips and jaw during speech (31). From this perspective, it would appear that complex movements such as speech are controlled through centrally generated motor commands that contain inherent provisions for afferent modification of the evolving motor output. That is, peripheral afferent input is utilized by central neural centers to set up the initial parameters of the motor program and, once established, afferent-dependent mechanisms, operating as part of the program, ensure achievement of multimovement goals.

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