

Kinematic and electromyographic responses to perturbation of the jaw^{a)}

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The task-dependent organization of sensorimotor mechanisms during the production of speech was investigated using a perturbation paradigm. Six subjects received unanticipated jaw perturbations before and during tongue elevation for [ædæ], in which the lips do not participate, and bilabial closure for [æbæ], in which the tongue does not participate. A strain gauge system was used to monitor inferior–superior displacements of the upper lip, lower lip, and jaw, while hooked-wire electrodes monitored muscle activity in various muscles of the lips, jaw, and tongue. Results indicated significant compensatory kinematic adjustments to jaw perturbations in the lips and/or jaw during [æbæ], but no labial compensations during [ædæ] (with the exception of one subject). EMG responses were inconsistent and not necessarily indicative of the kinematic findings. Individual subjects responded to perturbations reliably but differently, using different combinations of involved articulators to achieve bilabial closure and lingua–alveolar contact. The current study supports earlier research which suggests that the components of the motor system are flexibly assembled, based on the requirements of the specific task. That is, compensatory responses to sensory information occur only when such responses are functionally necessary.

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INTRODUCTION

Even the simplest speech sounds require the coordination of numerous articulatory components, including the lips, tongue, jaw, and velum. Differences in the configuration and sequencing of the articulators provide the large set of vocal tract gestures underlying the phonetic elements of a given language. The general nature of the neural mechanisms underlying this large set of vocal tract configurations is just beginning to be understood. For example, some studies have demonstrated that multiarticulate speech movements are coordinated via sensorimotor linkages among both local and remote components of a complex motor behavior (Abbs and Gracco, 1984; Folkins and Abbs, 1975, 1976; Folkins and Zimmermann, 1982; Gracco and Abbs, 1985). Experimentally, this is illustrated when a component of a compound, multiarticulate speech action is disrupted and both remote and local structures compensate for the perturbation. Abbs and Gracco (1984) and Gracco and Abbs (1985) studied such effects using perturbations of the lower lip during bilabial closure for [aba]. They observed local (or “autogenic”) compensations in the perturbed lower lip in the form of increased EMG activity and movement displacements, durations, and velocities. They also noted remote (or “nonautogenic”) compensations in the nonperturbed upper lip, reflecting coordinated sensorimotor linkages of the gestures for the two lips.

The coordination between the upper and lower lips observed by Gracco and Abbs does not appear to be “hard-wired,” but rather, specific to the bilabial task required of the lips. Abbs *et al.* (1985) demonstrated such task-specific sensorimotor processes by comparing labial responses to perturbations of the lower lip for [apa] to those for [afa]. In the [apa] bilabial task, where both the lower lip and upper lip coordinate to produce closure, the upper lip exhibited increased displacement when the lower lip was perturbed. Conversely, in the production of [afa], where upper lip movement is not usually required, perturbation of the lower lip resulted in no change in upper lip behavior. Such studies suggest that the sensorimotor mechanisms involved in the coordination of complex, multiarticulate speech movements are implemented in a functional, task-specific manner.

Task-specific sensorimotor compensations to dynamic perturbations during speech were originally observed by Kelso *et al.* (1984), who administered jaw perturbations during productions of the final consonants in [bæb] and [bæz]. Consistent with task-specific coordination, labial compensations were observed for perturbations administered during [bæb] (where labial activity is a necessary component of bilabial closure), but not during [bæz] (where labial activity is not necessary for generating the articulatory configuration for /z/).

Task-specific sensorimotor mechanisms have long been implicated in complex nonspeech motor behaviors, including maintenance of posture (Marsden *et al.*, 1981; Nashner, 1976), locomotion (Quintern *et al.*, 1985), and hand movements (Cole *et al.*, 1984; Traub *et al.*, 1980). The manner in which afferent information is used to coordinate such complex nonspeech movements has also been investigated using

^{a)} This article is based on the author's unpublished doctoral dissertation through the Department of Communicative Disorders, University of Wisconsin—Madison, Madison, WI (1988).

perturbation paradigms. For example, in a study involving complex hand coordination, Cole *et al.* (1984) observed task dependency in coordinated movements of the thumb and index finger. When a load was presented to the thumb during coordinated thumb–finger pinch tasks, nonautogenic compensatory responses were observed in the index finger. But, when the thumb was loaded in a task requiring thumb flexion with the index finger isometrically flexed against a mechanical stop, no response was noted in the index finger. Such a finding demonstrates that task-dependent sensorimotor mechanisms are a hallmark of complex motor behaviors in general, whether they be of speech or nonspeech movements.

Both the nonspeech and speech studies suggest that sensorimotor mechanisms are continually being reorganized into functional, task-specific units, in which only those structures required in the current complex motor behavior are actively coordinated. Such units have been termed “coordinative structures” or “functional synergies” (Bernstein, 1967; Fowler *et al.*, 1980; Kelso *et al.*, 1980; Kelso *et al.*, 1983). As noted by Kelso (1986), “most interesting for the coordinative structure hypothesis is that ... responses occur only if they perform a useful *function* and they are flexibly tuned to that function” (p. 120).

The purpose of the current investigation was to extend the Kelso *et al.* (1984) study to determine if sensorimotor mechanisms are organized in a task-dependent manner during the production of speech. This was done as part of a larger study (Shaiman, 1988) examining these mechanisms across a variety of speech tasks. More specifically, responses to perturbations of the jaw during the production of [æbæ] and [ædæ] were compared. The existence of numerous articulatory degrees of freedom allowed for perturbation compensations to occur with varying involvement of the upper lip, lower lip, and jaw during the production of [æbæ], and of the jaw and tongue during [ædæ]. Therefore, if task-dependent coordinative structures are in operation, jaw perturbations were expected to result in significant upper lip, lower lip, and/or jaw compensations (but with no lingual responses) during [æbæ], since the lips and jaw, but not the tongue, are involved in the articulatory constriction for /b/. Conversely, jaw perturbations were expected to result in significant lingual and/or jaw compensations during [ædæ], but with no changes in labial activity, since the lips are not involved in the articulatory constriction for /d/.

I. METHODS

A. Subjects

Subjects were six normal adult females, ranging in age from 18–30 years. Subjects were screened (via self-report) to be free of neurological and speech and hearing difficulties. Subjects were naive as to the objectives of the experiment and to the procedures used in motor control and speech physiological research.

B. Jaw perturbations

Unanticipated perturbations were applied to the jaw in an inferior direction, using a linear motor. Schematically

depicted in Fig. 1, the shaft of the linear motor was coupled, via a wire and pulley system, to a custom-fitted dental splint, produced for each subject by a prosthodontist.¹ A load cell located near the tip of the motor's shaft was used to transduce force, providing sensitivity as small as 1 g. The linear motor operated under force feedback control, following speech movements at constant, nonelastic tracking loads of 20 to 30 g.

C. Movement transduction

To minimize head movement, the subject's head was stabilized using a cephalostat mounted to the back of a dental chair (Abbs and Stivers, 1978). Inferior–superior movements of the upper lip, lower lip plus jaw, and jaw were transduced using a cantilever beam strain gauge transduction system (Barlow *et al.*, 1983; Muller and Abbs, 1979) mounted onto the cephalostat. The lower lip movement signal was obtained by digitally subtracting the jaw signal from the combined lower lip plus jaw signal. The response characteristics of the strain gauge transducers were linear over a range of ± 2 cm, with a flat frequency response from dc to 20 Hz.

Despite tight securing of the head in the cephalostat, jaw perturbations resulted in small, inferiorly directed movements of the head. This head movement appeared as artifactual displacements in the movement signals of the articulators. In order to measure and adjust for this head

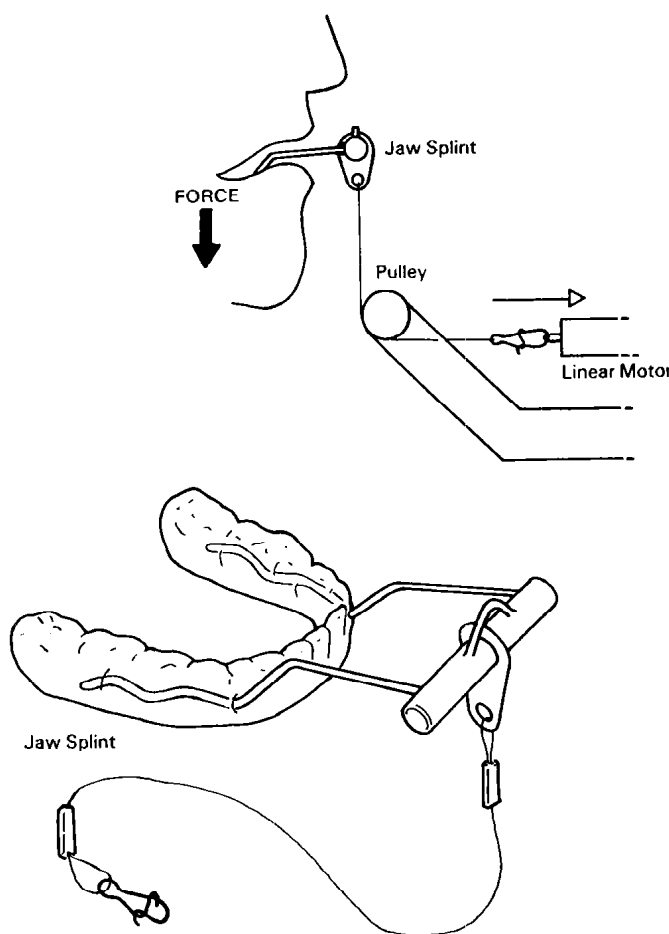


FIG. 1. Schematic drawing of linear motor and custom-fitted dental splint for jaw perturbations.

displacement, a cantilever beam strain gauge transducer was attached to the bridge of the subject's nose. This signal was then digitally subtracted from the upper lip, lower lip, and jaw signals.

No direct measure of tongue kinematics was made. Tongue EMG activity alone (see below) was used to determine lingual responses to perturbations.

Movement signals were digitally filtered prior to analysis, using a four-pole, 20-Hz low-pass Butterworth-like filter implementation.

D. Electromyography

By means of bipolar hooked-wire electrodes, EMG was recorded from: orbicularis oris superior (OOS), orbicularis oris inferior (OOI), mentalis (MTL), depressor anguli oris (DAO), superior longitudinal (SL), anterior portion of genioglossus (GG), and medial pterygoid (MPT). Each wire of an electrode pair was inserted separately, using a 30-gauge hypodermic needle. Electrode placements and confirmations were based on previous anatomic and physiologic descriptions (Hirose, 1971; Kennedy and Abbs, 1979; MacNeilage and Sholes, 1964; Miyawaki *et al.*, 1975; and Sussman *et al.*, 1973).

The EMG signals were preamplified with a passband of 22 Hz to 22 kHz, with additional amplification using a passband of 50 Hz to 2.5 kHz prior to computer digitization.

E. Movement tasks

Subjects were instructed to take a deep breath and sustain the vowel [æ]. Upon hearing a tone, they were to produce the sound [bæ] (or [dæ]) as quickly as possible, and then resume the sustained [æ]. Subjects were not informed of the possibility of jaw perturbations. Counterbalanced groups of subjects began with either [æbæ] or [ædæ]. Each perturbed or "load" trial and the unperturbed "control" trial immediately preceding it were digitized. Five control-load pairs of an utterance were obtained before changing to the alternate utterance. Approximately 50 control-load pairs for each utterance were obtained for each subject.

In order to minimize the effects of head movement, subjects were provided with a continuous oscilloscopic display of their head movements. Subjects were instructed to maintain their head movement signal at the horizontal cursor indicated at the center of the screen. Additionally, the oscillographic display was blanked out for a 500-ms period following each presentation of the tone, so that subjects could not observe any head displacement caused by the perturbation to the jaw.

F. Perturbation characteristics

The linear motor delivered inferiorly directed loads to the jaw, with a force magnitude of 0.45 N, and a rise time of 20 ms. These load characteristics were chosen to ensure that the resulting displacements and velocities were within the range of normal jaw movements for speech (Abbs, 1973; Abbs and Netsell, 1973). Thus, unlike the Kelso *et al.* (1984) study, the magnitude of the perturbations in the current study was not large enough to inhibit the jaw from

responding to or compensating for the load. In this way, autogenic responses of the jaw to jaw perturbations, as well as nonautogenic lip and tongue responses, were possible.

Perturbations were randomly introduced, based on a computer table, on 15% of the trials to minimize adaptation to, or anticipation of, the perturbations (Abbs and Gracco, 1984). The low perturbation rate ensured that the subjects were not responding defensively in anticipation of the perturbations. The target interval for loads was a 100-ms interval centered on the onset of medial pterygoid EMG activity associated with jaw elevation for /b/ or /d/. The experimenter, via computer, was able to manually control the time of onset of the perturbation. By observing the onset of muscle activity relative to the onset of the stimulus tone, it was possible to introduce perturbations during the 100-ms target interval (cf. Gracco and Abbs, 1985).

G. Data recording and analysis

All signals were digitized on-line with 12-bit resolution on a DEC PDP-11/44 lab computer. EMG activity was digitized at 2800 samples/s, while movement and force signals were digitized at 400 samples/s. Following acquisition, the data were transferred to a SUN Microsystems network for data analysis.

Computer algorithms provided the following measures (illustrated in Fig. 2): (1) time of load onset in relation to

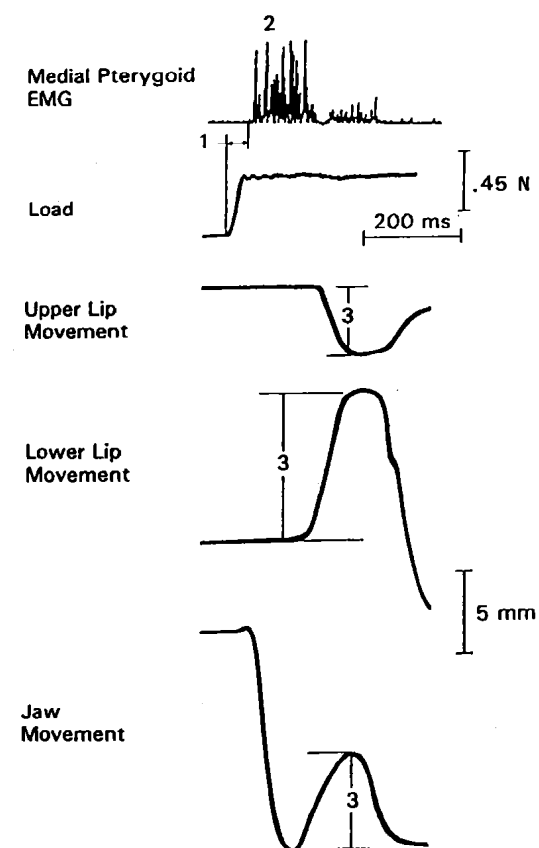


FIG. 2. Movement and EMG events used to derive the measured variables. See text for detail.

the onset of the phasic burst in medial pterygoid EMG activity; (2) area under the curve for the first 100 ms of the phasic EMG burst (rectified and smoothed) for all muscles; and (3) upper lip, lower lip, and jaw displacements, from onset to peak. Only the control-load pairs in which the time of load onset occurred within ± 50 ms of the onset of medial pterygoid EMG activity were subjected to statistical analysis.

H. Statistical procedures

A two-way analysis of variance, with repeated measures, was performed on the group data for each of the dependent variables. The two main factors were utterance ([æbæ] vs [ædæ]) and condition (control versus load). When the F value for the utterance-by-condition interaction was significant, subsequent tests of simple effects (Kirk, 1982) were performed to determine significance of control-load differences within an utterance type. Due to differences in how subjects responded to perturbations, additional analyses were performed for each individual subject, using two-tailed paired t tests. The alpha level for all statistical procedures was $p < 0.01$.

II. RESULTS AND DISCUSSION

It was initially established that the perturbations did, in fact, displace the jaw in space, relative to an arbitrary reference point. That is, the position of the jaw in space at the onset of elevation for both utterances was significantly lower [$F(1,5) = 29.72, p = 0.0028$] for load trials than for control trials. This lowering of the initial position of the jaw established the need for compensatory displacement increases in order to attain either bilabial closure or lingua-alveolar contact. The group data for the position of the jaw at the comple-

tion of elevation indicated no significant difference [$F(1,5) = 11.96, p = 0.181$] between control and load trials.

Overall, the results demonstrated that sensorimotor mechanisms are organized in a task-dependent manner for the production of speech. Results consistent with such organization were observed in five of the six subjects studied. This was indicated primarily by the presence of labial kinematic compensations during [æbæ], coupled with the absence of labial compensations during [ædæ]. However, as will be described later, there were also important individual differences in how subjects compensated for perturbations, as well as differences in the degree to which EMG results reflected compensations.

The analysis of the group lower lip displacement measures indicated an utterance by condition interaction [$F(1,5) = 20.76, p = 0.006$], providing evidence supporting task-dependent organization. Lower lip displacements increased significantly [$F(1,5) = 56.16, p < 0.001$] for perturbed trials during the production of [æbæ], in which both the upper lip and lower lip are involved. Conversely, lower lip displacements showed no significant difference [$F(1,5) = 1.10, p > 0.05$] between control and load trials during the production of [ædæ], in which the lips are *not* involved. This finding is consistent with the expectation that compensatory labial responses will be task specific. That is, compensations will occur only when they serve a useful function. Compensatory lower lip responses do not appear to occur during a movement task in which the lips are not involved.

None of the remaining interactions in the ANOVAs (i.e., utterance by condition) indicated significant differences between control and load trials for productions of

TABLE I. Mean jaw positions and standard deviations (in mm) relative to arbitrary reference point. Negative numbers indicate positions below the arbitrary reference point.

Subject	Utterance	Onset of closure		Closure	
		Control	Load	Control	Load
1	æbæ	0.11(0.17)	-1.64(0.62) ^a	1.98(1.56)	0.22(1.49) ^a
	ædæ	0.04(0.12)	-1.41(0.42) ^a	1.82(1.09)	0.02(1.14) ^a
2	æbæ	0.09(0.12)	-2.70(1.03) ^a	7.50(1.50)	7.50(2.07)
	ædæ	0.09(0.10)	-2.60(0.93) ^a	8.11(2.23)	7.61(2.32)
3	æbæ	0.09(0.09)	-6.14(1.81) ^a	6.14(2.09)	6.40(1.92)
	ædæ	0.13(0.23)	-4.85(1.88) ^a	9.21(2.91)	7.26(3.06) ^a
4	æbæ	0.09(0.92)	-4.51(1.58) ^a	5.59(1.77)	5.17(3.08)
	ædæ	0.11(0.13)	-4.31(1.37) ^a	7.30(1.97)	5.76(3.61) ^a
5	æbæ	0.05(0.07)	-3.06(1.42) ^a	6.35(2.46)	3.35(3.28) ^a
	ædæ	0.02(0.07)	-2.87(1.38) ^a	8.85(1.58)	5.24(2.81) ^a
6	æbæ	0.03(0.08)	-2.36(1.32) ^a	4.12(0.95)	2.30(1.37) ^a
	ædæ	0.00(0.10)	-2.29(1.16) ^a	3.88(1.08)	1.76(1.25) ^a

^a $p < 0.01$ for control - load comparisons.

[æbæ] vs [ædæ]. This appears to be due to individual subjects responding to the perturbations in reliable but subject-specific ways. This is, perhaps, not surprising since the tasks allowed for a variety of compensatory responses among the involved articulators. The responses exhibited by the six subjects fell into three different categories, based on the kinematic responses to jaw perturbations: (1) nonautogenic responses, observed in subjects 1, 5, and 6; (2) autogenic responses, observed in subject 2; and (3) both autogenic and nonautogenic responses, observed in subjects 3 and 4.

A. Nonautogenic responses

1. Kinematics

Three subjects, 1, 5, and 6, exhibited predominantly nonautogenic kinematic compensations to jaw perturbations. That is, adjustments occurred in components of the complex behavior that were *not* directly disturbed (i.e., the lips or tongue), rather than in the jaw, which was perturbed. Task specificity would be revealed by the presence of labial displacement increases from control to load trials during the production of [æbæ], and the absence of labial displacement increases during the production of [ædæ]. Two of the three subjects in this group demonstrated task-specific kinematic compensations.

It should be noted that the perturbations did significantly displace the jaw in space for these three subjects. Table I shows the mean positions of the jaw in space at the onset of jaw elevation and at the point of jaw closure, relative to an arbitrary reference point, for each of the six subjects. For the subjects demonstrating nonautogenic responses (1, 5, 6), the perturbations significantly lowered the starting point of jaw elevation for both utterances. Importantly, however, the position of the jaw at the point of closure was also significantly lower for load trials than for controls. This overall lowering of the jaw position presumably resulted in the need for increases in upper and/or lower lip displacements in order to achieve bilabial closure for [æbæ], and increases in tongue displacement to achieve lingua-alveolar contact for [ædæ].

Task specificity was observed in the nonautogenic responses of subjects 1 and 6. Figure 3 depicts the average load-minus-control differences in millimeters for the upper lip, lower lip, and jaw displacements during productions of [æbæ] (white bars) and [ædæ] (hatched bars). As can be seen, subjects 1 and 6 both demonstrated significant displacement increases from control to load trials in the lower lip and/or upper lip to jaw perturbations during the production of [æbæ]. As noted previously, no compensations were observed in the jaw. Therefore, for these two subjects, the lips, rather than the jaw, compensated to attain bilabial closure. Conversely, for productions of [ædæ], the same subjects (1 and 6) demonstrated either no difference in labial displacements between control and load trials, or a significant decrease in labial displacements for perturbed trials. During [ædæ], it is possible that tongue displacement may have increased to compensate for the lowered jaw position; however, the lack of tongue kinematic data makes this only conjecture. The responses of these two subjects, therefore,

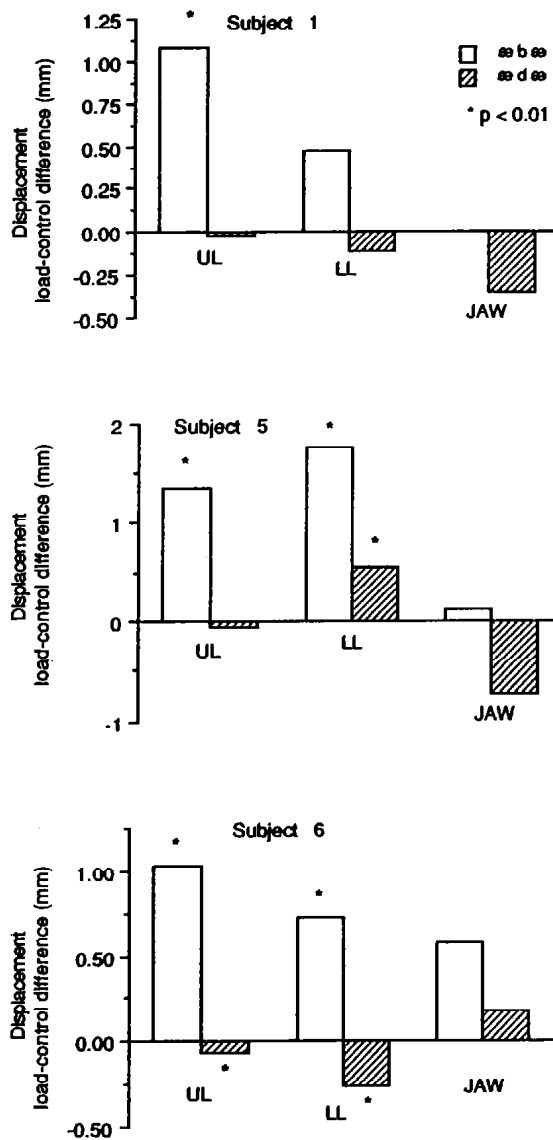


FIG. 3. Mean displacement load-minus-control differences of the upper lip, lower lip, and jaw, during productions of [æbæ] and [ædæ] for subjects demonstrating nonautogenic responses.

support the hypothesis of task specificity, since kinematic compensations were observed only when they were functionally appropriate.

Subject 5 also exhibited nonautogenic kinematic responses to jaw perturbations. However, her responses did not support the hypothesis of task specificity. Although she similarly demonstrated significant labial displacement increases during [æbæ], as seen in Fig. 3, she also exhibited a significant increase in lower lip displacement for perturbed trials of [ædæ]. Such a labial displacement increase during a task not involving lower lip elevation argues against task specificity. It should be noted that the mean increase in lower lip displacement to load trials for [ædæ] for subject 5 was only 0.54 mm greater than control trials, and that this resulted in a mean displacement of only 1.10 mm for load trials. Therefore, this was a very minimal contribution of the lower lip to the articulatory constriction during perturbed trials of [ædæ].

2. Electromyography

The EMG responses for individual subjects indicated that muscles expected to show an increase in activity to perturbations during a given utterance occasionally did not demonstrate significant increases. Conversely, muscles expected to show no increase in activity often did demonstrate significant increases. Additionally, increases in muscle activity were not always characterized by parallel kinematic changes in the respective structures. As noted by numerous researchers (e.g., Baken, 1987; Loeb and Gans, 1986), the kinematics of a structure are not always causally related to the magnitude of the EMG signal.

This incongruity between muscle activity and movement is exemplified by the EMG responses of subject 6 to perturbations, as seen in Fig. 4. Depicted are the mean EMG

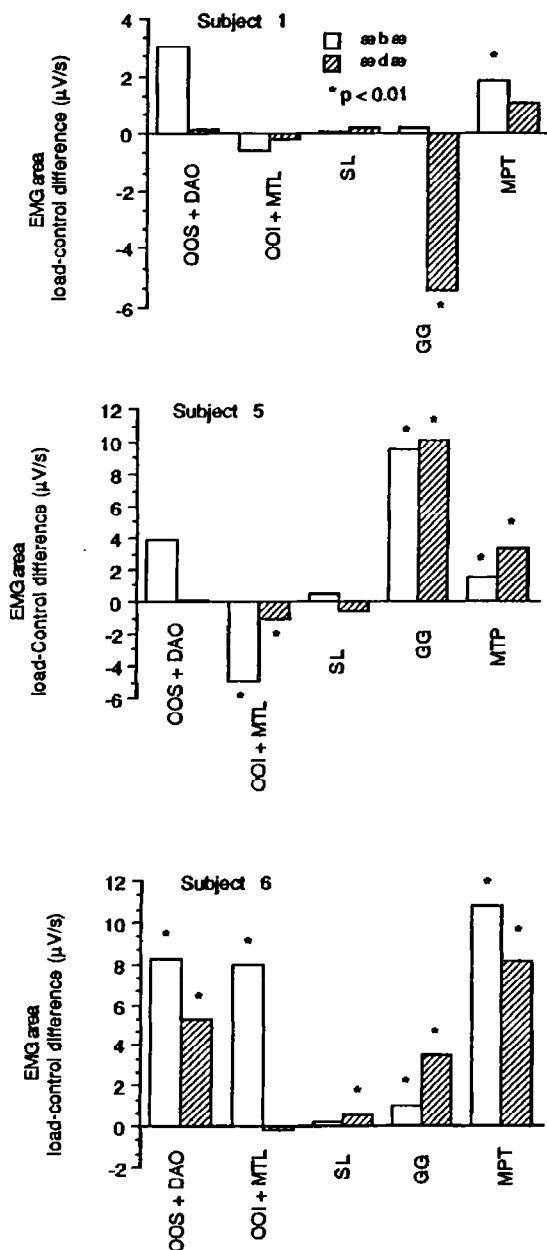


FIG. 4. Mean EMG area load-minus-control differences during productions of [æbæ] and [ædæ] for subjects demonstrating nonautogenic responses.

area load-minus-control differences for muscles of the upper lip (OOS + DAO), lower lip (OOI + MTL), tongue (SL and GG) and jaw (MPT), for [æbæ] (white bars) and [ædæ] (hatched bars). The combined activity of OOS + DAO and OOI + MTL is presented because these muscle pairs are synergistic in depressing the upper lip and elevating the lower lip (Sussman *et al.*, 1973; Folkins and Abbs, 1976), respectively. Additionally, the combined data were usually indicative of the responses of each muscle individually.

For subject 6's productions of [æbæ], it can be seen that upper and lower lip EMG activity increased appropriately, corresponding to the kinematic increases. However, MPT activity also increased, despite no significant change in the jaw kinematics to perturbations. Contrary to the hypothesis, GG activity also increased for perturbed productions of [æbæ]. However, since no measure of lingual kinematics is available, it is impossible to determine if such EMG increases were accompanied by parallel kinematic increases. Conversely, during the production of [ædæ], upper lip EMG activity increased significantly despite a significant decrease in upper lip displacement to perturbations. Similarly, MPT activity again increased significantly, despite no change in jaw displacement during [ædæ].

Similar inconsistent electromyographic findings were observed for all subjects, indicating that muscular responses were often *not* indicative of kinematic responses. This suggests that EMG area measurements are not a valid method of determining compensations to perturbations.

B. Autogenic responses

1. Kinematics

Subject 2 exhibited kinematic responses that were predominantly autogenic in that the perturbed structure (i.e., the jaw) demonstrated the primary compensation. Although it was initially thought that only the upper lip and/or lower lip would compensate for perturbations during [æbæ], it is not surprising that, in some subjects, the primary compensation may be autogenic. This finding of jaw compensation supports the hypothesis of task dependency, since only a structure involved in each task (in this case, the jaw) compensated for perturbations.

The need for compensation was demonstrated by significant decreases in the starting position of the jaw for perturbed trials relative to control trials for both utterances (see Table I). For subject 2, the position of the jaw at the point of closure was approximately equal for control and load trials. This indicates that although jaw elevation started at a lower position in space for perturbed trials, it moved further in order to attain the same position as when unloaded.

Task specificity can be observed in subject 2 by the presence of significant jaw displacement increases for perturbed trials of both [æbæ] and [ædæ], as seen in Fig. 5. The lower lip did not exhibit control-load differences for either utterance. Contrary to expectations, upper lip displacement did increase significantly for [ædæ]; however, this was a mean increase of only 0.14 mm, resulting in a mean displacement of 0.16 mm, and is within the measurement error range of the transducers. Upper lip displacement did not increase for

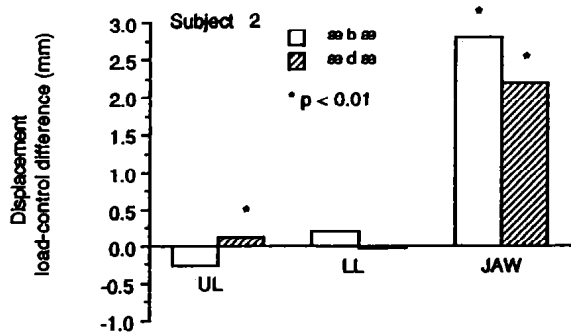


FIG. 5. Mean displacement load-minus-control differences of the upper lip, lower lip, and jaw during productions of [æbæ] and [ædæ] for the subject demonstrating autogenic responses.

productions of [æbæ]. Such findings support the hypothesis, since physiologically significant compensations were observed only in a structure actually involved in each task.

2. Electromyography

The EMG responses of subject 2 were somewhat more consistent with the kinematic findings than those of the previously discussed subjects. As seen in Fig. 6, MPT activity provided the primary muscular compensation for both utterances. This finding paralleled the kinematic data, in which increases in jaw displacements provided the primary kinematic compensations. The lack of increased labial EMG activity during [æbæ] further paralleled the kinematic data, supporting the need for a robust autogenic compensation of the jaw. Paradoxically, GG activity increased significantly for both utterances. Since no measure of tongue kinematics was available, it cannot be determined if these EMG increases resulted in kinematic compensations, or merely stiffening of the tongue.

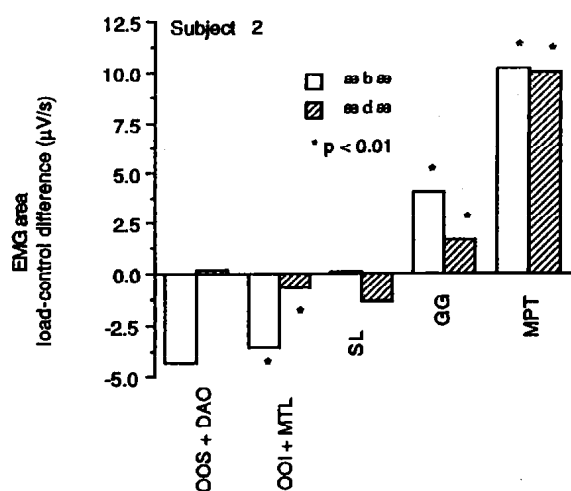


FIG. 6. Mean EMG area load-minus-control differences during productions of [æbæ] and [ædæ] for the subject demonstrating autogenic responses.

C. Autogenic and nonautogenic compensations

1. Kinematics

Two subjects, 3 and 4, exhibited both autogenic and nonautogenic compensations to jaw perturbations. That is, compensations to jaw perturbations were observed in both the upper and/or lower lips (nonautogenic) and the jaw (autogenic). Task specificity would be demonstrated by the presence of displacement increases to perturbed trials in the upper and/or lower lips and jaw during the production of [æbæ], and displacement increases in only the jaw during [ædæ]. Both subjects displayed this pattern of compensations.

The need for compensation was reflected in significantly lower onset positions of the jaw during loaded gestures (see Table I). For [æbæ], the jaw was able to elevate to a level comparable to that of control trials, while for [ædæ], the jaw elevated to a position in space somewhat lower than for control trials.

Kinematic changes were organized in a task-dependent manner for both subjects. The displacement changes for [æbæ], seen in Fig. 7, indicated significant autogenic compensation by the jaw as well as nonautogenic compensation by the lower lip. Also, subject 3 demonstrated significant upper lip compensations to loads. Conversely for [ædæ], whereas the jaw displacements increased significantly, the labial displacements either remained constant or decreased significantly. However, despite significant increases in jaw displacements, the perturbed jaw did not compensate to a position comparable to control trials for [ædæ]. This sug-

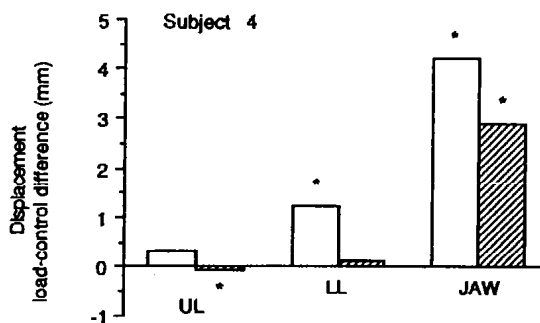
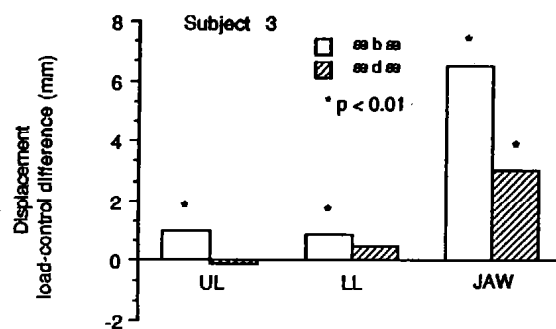


FIG. 7. Mean displacement load-minus-control differences of the upper lip, lower lip, and jaw, during productions of [æbæ] and [ædæ] for subjects demonstrating both autogenic and nonautogenic responses.

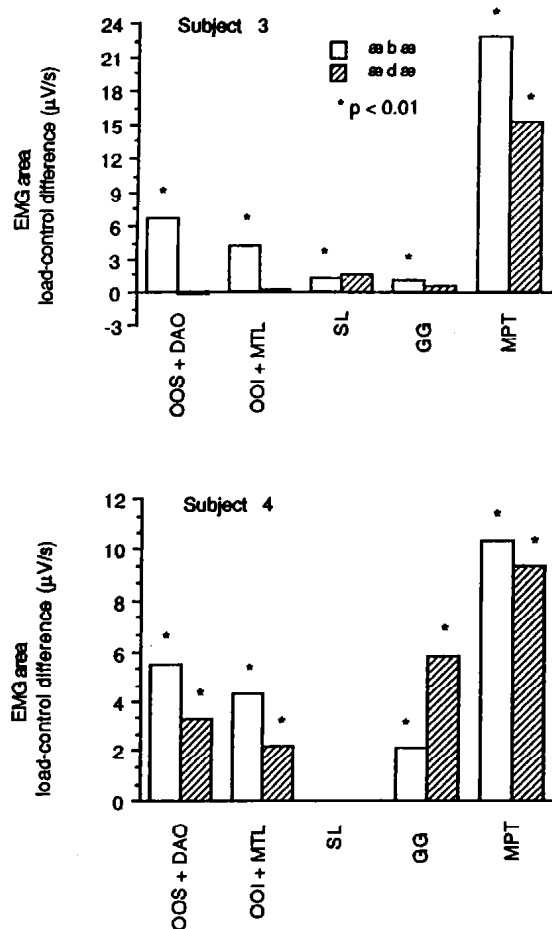


FIG. 8. Mean EMG area load-minus-control differences during productions of [æbæ] and [ædæ] for subjects demonstrating both autogenic and nonautogenic responses.

gests that (nonautogenic) tongue elevation may have combined with jaw displacement to compensate for the load.

2. Electromyography

The EMG responses of subjects 3 and 4 were relatively inconsistent with the kinematic findings, as observed in Fig. 8. For example, subject 4 demonstrated increased EMG activity in all muscles during both utterances. This was evident despite no difference between control and load trials for upper lip displacement during [æbæ], and a significant de-

crease in upper lip displacement during [ædæ]. These findings provide further evidence that EMG activity is not necessarily indicative of kinematic responses.

III. GENERAL DISCUSSION

A summary of kinematic responses observed in the current study is provided in Table II. Overall, the results suggest that sensorimotor mechanisms involved in speech motor control operate in a task-dependent manner. That is, compensatory responses to jaw perturbations were selectively organized, based on the requirements of the speech task, so that only those movements specific to the goal were coordinated. This conclusion is consistent with previous studies showing task-dependent sensorimotor control of speech (Abbs *et al.*, 1984; Abbs *et al.*, 1985; Kelso *et al.*, 1984; Munhall and Kelso, 1985). In particular, the current experiment provides both a replication and extension of the Kelso *et al.* (1984) study. Despite current refinements in methodology, the results of both experiments are essentially the same. That is, jaw perturbations result in task-specific labial responses, occurring only during the appropriate speech motor behavior.²

The presence of compensations during the production of [æbæ] in the current experiment indicates that all subjects achieved bilabial closure, albeit through varied methods of compensation. These varied responses are not a surprising finding; earlier studies have also demonstrated various combinations of autogenic and nonautogenic responses to perturbations. For example, Gracco and Abbs (1985) observed both autogenic and nonautogenic compensations to perturbations of the lower lip during bilabial closure for [apa]. In the current study, two subjects, 4 and 5, demonstrated both autogenic (jaw) and nonautogenic (upper lip and/or lower lip) compensations during bilabial closure for [æbæ]. However, there were a variety of other types of compensation demonstrated by the remaining subjects. Subjects 1, 5, and 6 all demonstrated predominantly nonautogenic (upper and/or lower lip) compensations to jaw perturbations during [æbæ]. This is comparable to the findings of Folkins and Abbs (1975, 1976) and Folkins and Zimmermann (1982), who reported only nonautogenic compensations during bilabial closure tasks. Subject 2 in the current study also achieved bilabial closure. However, unlike prior

TABLE II. Summary of responses to jaw perturbations.

	Nonautogenic	Autogenic	Nonautogenic and autogenic
Subject description	Subjects 1 and 6 showed labial compensations during [æbæ] but not during [ædæ]. Subject 5 showed labial compensations during both utterances.	Subject 2 showed primary compensation to the disturbed structure, the jaw, during [æbæ] and [ædæ].	Subjects 3 and 4 showed both labial (nonautogenic) and jaw (autogenic) compensations during [æbæ], and jaw compensations during [ædæ].
Support for task-dependency hypothesis	yes (1 and 6) no (5)	yes	yes

studies, subject 2 utilized predominantly autogenic jaw compensations to respond to the perturbations during the production of [æbæ], with no contribution from the nonautogenic upper and lower lips. The responses of this subject thus indicate a previously unobserved (but not unreasonable) method of compensating for perturbations, i.e., the perturbed structure achieves compensation by itself.

Differing methods of compensation among subjects reflect the complexity of nervous system organization, especially as articulatory complexity increases. The effect of decreased articulatory complexity is particularly evident when movement of an articulator is restricted, for example, by placing a bite block between the teeth to inhibit jaw movement. In such cases of reduced articulatory complexity, compensation behaviors are more similar across subjects, due to the limited number of articulators contributing to the intended movement (Shaiman and Abbs, 1987; Shaiman, 1988). In the current study, greater heterogeneity of compensatory responses was observed due to increased articulatory complexity.

A. Theoretical implications

In early models of speech production, the movements specific to a goal were thought to be planned in terms of absolute spatial targets or "points specified within an internalized space coordinate system" (MacNeilage, 1970). Evidence against such an internalized spatial reference is provided in the current study. For example, the spatial position of the jaw at the point of closure for [æbæ] was not necessarily the same for control and load trials; i.e., bilabial closure did not occur at a fixed, specified position in space. Kelso *et al.* (1984) reported similar findings in their jaw perturbation study, as have several other researchers, who have suggested alternative goals, including patterns of articulatory contact, levels of intraoral air pressure and airflow, and auditory-perceptual goals (Ladefoged *et al.*, 1972; MacNeilage, 1980; Perkell, 1980, 1981). Although the findings of the current study do not clearly point to the nature of the articulatory "goal" in speech, they do suggest that variable movement interactions among articulators are organized to produce relatively stable acoustic-perceptual results (i.e., motor equivalence). Despite differences in the spatial and temporal characteristics of how bilabial contact is achieved (Gracco and Abbs, 1986), the perceptually salient characteristics of the acoustic output are realized.

Despite the fact that a goal (e.g., an acoustic pattern) may be fixed or preprogrammed, the method of accomplishing that goal, through sensorimotor coupling of articulators, is not fixed, but rather, flexibly coordinated to produce the intended outcome. Numerous researchers have posited that processes exist that flexibly couple the motor system into coordinated groupings of muscles or structures that are constrained to behave as a task-specific, functional unit. Such an organization has been termed a "coordinative structure" or a "functional synergy" (Bernstein, 1967; Fowler *et al.*, 1980; Kelso *et al.*, 1980; Kelso *et al.*, 1983). It has been suggested that compensation is characteristic of this flexible coupling, and that compensatory interactions are representative of the normally occurring interactions among articulators in non-

perturbed speech (Folkens and Linville, 1983; Kelso *et al.*, 1984; Lindblom *et al.*, 1979; MacNeilage, 1981).

Various theories exist on how compensation is accomplished and the role peripheral feedback plays in achieving compensation. Perkell (1981) postulated that predictive, off-line feedback mechanisms are used to adjust the parameters of a central program to changes in the frame of reference. This is similar to a neural representation, which defines the current relationship between motor and sensory events, as suggested by Neilson and Neilson (1987). Such a central representation would most likely be generally and flexibly specified (e.g., Gracco and Abbs, 1985) and based on functional relationships among structures that need to be coordinated for a given motor behavior. Once these flexible sensorimotor "pathways" are centrally established for a given movement, on-line, moment-to-moment peripheral afferent information appropriate to the specific movement would be utilized to adjust for ongoing disturbances. However, only feedback specific to the goal of the utterance would be incorporated into the compensation. The present data reflect such a task-oriented organization in which only the necessary components are marshalled together, in a "functional synergy," for the accomplishment of a multimovement goal.

It has been suggested that the observed compensatory responses may be mediated by brain-stem reflex pathways (Weber and Smith, 1987). Furthermore, Smith *et al.* (1985) suggested that the perioral reflex is not suppressed during speech. Although latencies were not measured in the current study, it can be assumed that they would be somewhere within the range of those reported in previous experiments (22 to 75 ms, Abbs and Gracco, 1984; 20 to 30 ms, Kelso *et al.*, 1984), given similar methodologies across studies. However, there are several considerations for why the labial responses, in particular, were not reflexive. In the current study, the jaw was loaded, with responses of the lips and tongue being of primary interest.³ In a study by Weber and Smith (1987), a jaw closing muscle was mechanically stimulated during a static nonspeech task, with no reflex responses observed in the labial or lingual musculature. Since stimulation of a jaw muscle resulted in no modulation of labial muscles, it can be assumed that the labial responses observed in the current study were not reflexes, but rather, voluntary compensations to the jaw perturbations. Hypothetically, the perioral reflex could be elicited in the current study by labial stimulation. However, as noted in Sec. I, the dental splints were fabricated so as to eliminate contact of the splint wires with the lower lip during movement toward bilabial closure (see footnote 1). This construction ensured that the perioral reflex was not elicited by jaw perturbations. Furthermore, in the current study, there is no implication that the perioral reflex is suppressed. Rather, it is suggested that the perioral reflex is merely not elicited by jaw stimulation. Because a reflex response in the lips is not elicited via jaw stimulation, this implies that the labial compensations in the current study were voluntary responses. It also appears that labial responses were not time locked to the load onset. Robust compensatory labial responses during production of [æbæ] were observed for all subjects (except subject 2) for perturbations occurring at any time within the 100-ms target inter-

val. This indicates that responses occurred regardless of when the load was introduced relative to the onset of EMG activity, providing further support for compensations being under voluntary, higher level control (Abbs and Gracco, 1984; Gracco and Abbs, 1985). However, as noted by Kelso *et al.* (1986), "functional cooperativity—not the neural mechanism *per se*—is fundamental" to the concept of coordinative structures (p. 33).

The results of this study support the findings of Kelso *et al.* (1984) and suggest that the control mechanisms for speech production are intrinsically task specific. Varying contributions of the involved articulators to the compensatory action reflect the permutability of the motor system during complex behaviors. This indicates that the components of the motor system are rapidly and flexibly assembled, based on the requirements of the specific task.

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¹The dental splints were fabricated for each subject so that the orthodontic wire projections were bent up at a 45-deg angle and then horizontally. This precluded contact of the wires with the lower lip during movement toward bilabial closure. Therefore, perturbations resulted in no contact of the wire to the lower lip, except at the time of bilabial closure. Since loads were introduced within ± 50 ms relative to the onset of MPT activity, any contact of the wires with the lower lip occurred well after the load onset and any subsequent response to the load.

²Despite the implications of the current experiment, there are a few limitations which warrant consideration. In particular, movements of the upper lip, lower lip, jaw, and head, performed with cantilever beam strain gauges, were transduced in only the inferior–superior dimension. This is problematic, in that articulatory movement has been described in both the vertical and horizontal planes, both in the lips (e.g., Abbs and Gilbert, 1973) and in the jaw (e.g., Gibbs and Messerman, 1972; Howell, 1987). For the lips, this is not a major problem, since the primary movement for these particular speech tasks is within the vertical plane. However, jaw movement during speech occurs in both horizontal and vertical planes, due to rotation of the jaw about the condyle, in a hingelike fashion. Measurement in only the vertical plane may ignore a substantial component of the jaw movement, namely, anterior–posterior movement (Westbury, 1988). Future studies are warranted in which movement is measured in additional planes.

Another limitation of the current study involves the lack of direct evidence for task specificity during the production of [ædæ]. Direct evidence would be provided by the presence of lingual compensations during [ædæ]. This was attempted by the use of electromyographic data. However, as indicated, EMG responses were often not indicative of kinematic responses. Therefore, increases in tongue displacements during [ædæ] could only be assumed. Replication of this study using a system such as the x-ray microbeam (Nadler *et al.*, 1988) for studying tongue kinematics is thus warranted.

Finally, it is difficult to determine if the lack of compensation in a structure during a given utterance was actually due to task-dependent organization or inadequate motor neuron pool depolarization. Houk (1978) noted that the presence or absence of a response in a passive structure cannot be taken as evidence for gain control in multiarticulate movements. In the current study, responses to perturbations were examined in structures that were not phasically active in one of the two speech tasks. Due to this limitation, the results of the current study need to be interpreted cautiously. However, in the companion study (Shaiman, 1988), task specificity was observed in the form of compensatory responses in an articulatory struc-

ture (in this case, the lower lip) which was phasically active in both speech tasks.

³Since jaw displacement was disrupted, but not inhibited as in earlier studies (e.g., Kelso *et al.*, 1984), the jaw was able to compensate in *either* task. Because of this, jaw compensations were not of prime importance in demonstrating task dependency.

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