Lip and jaw interaction during speech: Responses to perturbation of lower-lip movement prior to bilabial closure

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Electrical stimulation was used to produce unexpected, involuntary depression of the lower lip in three normal young adults. Stimulation was timed to begin 500 to 40 ms prior to voice offset in [æp] and [ɪp]. Upper lip, lower lip, and jaw movements were measured with a strain gauge system. Movements in 104 syllables with lower-lip stimulation were compared to the preceding normal syllable. Both the jaw and upper lip compensated for the involuntary perturbations in lower-lip movement. Compensatory movements did not occur as additional, discrete gestures following stimulation onset, but appeared as an increase in the size of closing movements. Bilabial closure was produced at the typical time (within − 10 to + 20 ms of voice offset) in 68% of the perturbed syllables, but it was delayed (a mean of 61 ms) in the remaining 32%. Neither the incidence nor the magnitude of this delay appeared to be related to the jaw position at stimulation onset or to the time between stimulation onset and voice offset.

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INTRODUCTION

A major direction in the study of motor control systems has been investigation of when and how sensory information is involved in the organization and control of movement. One experimental approach has been to load or otherwise perturb the movement of a structure and observe the response to the change in peripheral conditions. Although the responses to a mechanical perturbation are often referred to as "compensatory," it is assumed that the processes underlying compensatory responses are representative of motor processes involved in more typical movements.

Loading paradigms have been used most often to study the compensatory properties of the same muscles or joints that have been loaded (Evarts and Tanji, 1976; Bizzi *et al.*, 1978; Marsden *et al.*, 1976; Gottlieb and Agarwal, 1979; Houk, 1978; Conrad *et al.*, 1974; Lee and Tatton, 1975; Kennedy, 1977). However, there also have been a number of experiments dealing with the compensatory responses in joints or structures other than those receiving the direct perturbation. The importance of interactive responses between different structures has received attention recently in the speech literature (Fowler *et al.*, 1980) and experiments on the compensatory responses between nonspeech structures may provide insight into similar processes in speech motor control.

One example of an interactive compensation between different structures has been reported by Polit and Bizzi (1978, 1979). In this experiment monkeys trained to move the arm to a target were able to do so regardless of postural changes or mechanical perturbation of arm position prior to movement. After sensory nerves were cut and the same postural changes were introduced the monkeys consistently missed the targets by an amount approximately equal to the postural change. Polit and Bizzi conclude that sensory information plays an important role in adapting the action of the arm relative to the spatial orientation of the body.

An important finding from the perturbation experiments is that compensatory responses may have characteristics that depend on the direction of the interaction. For example, although arm movements may be adjusted on the basis of body position, any effects of the monkey's arm on the orientation of the body might be substantially different from the body-to-arm effects documented by Polit and Bizzi (1978, 1979).

A number of studies have applied perturbations to locomotion in the intact cat (Forssberg, 1979; Prochazka *et al.*, 1978), decerebrate cat (Miller *et al.*, 1977), and spinal cat (Forssberg *et al.*, 1977; Grillner and Rossignol, 1978; Forssberg *et al.*, 1980). When the cat's ankle is stimulated compensatory responses have been studied in both the knee and hip of the same leg (Forssberg *et al.*, 1975) and also in the ipsilateral and contralateral legs (Forssberg *et al.*, 1977). Any leg can influence the activity in the other legs and interference at any joint may influence activity acting on other joints in the same leg. Therefore these studies illustrate an interdependence between some compensatory responses. That is, characteristics of structure A may influence structure B and structure B may also influence structure A. However, the influence of structure A on structure B may be very different from the influence of structure B on structure A.

In addition to the positional influences documented in the studies of cat locomotion, it has been shown that compensatory responses may be dependent on the timing of the perturbation. Forssberg *et al.* (1975) conclude, ". . . an identical tactile stimulus applied to the dorsum of the foot gives rise either to a marked flexion or a marked extension response depending entirely on the phase of the step cycle in which the stimulus occurs (p. 105)." Murakami *et al.* (1977) have shown an example of interactions between the lip and the jaw in the decerebrate rabbit. They stimulated the lip at different points in centrally elicited mastication and found that the interactive effects vary as a function of where in the chewing cycle the lip stimulation occurs.

Compensatory interactions have been shown also between different structures in speech motor control. For example, Lindblom *et al.* (1979) have illustrated

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that the tongue and lips can compensate regardless of the position at which the jaw is fixed with a bite block. Only sustained vowels were used in the Lindblom *et al.* study so there were no temporal requirements placed on the compensatory gestures. However, Folkins and Abbs (1975, 1976) applied unpredicted loads to oppose the upward movement of the jaw preceding and during bilabial closing movements. Compensatory EMG activity and compensatory lip movements were observed and bilabial closure was always achieved regardless of the interference with jaw movement.

From these studies it appears that during speech the movements of the upper and lower lips are produced in a manner dependent on the movement of the jaw. However, it is not clear whether this influence is unidirectional or bidirectional; that is, it is not known whether the movements of the jaw are also influenced by the peripheral conditions of lip movement. From an anatomical perspective it seems the lips would be more easily able to compensate for the jaw during speech than vice versa. For example, if the jaw were to compensate for the lips, then other structures such as the tongue, hyoid bone, or platoglossus muscles might also be influenced and further compensations would be necessary. However, from a physiological perspective there are a number of reflex studies showing that application of different types of stimuli to the lips will produce a short-latency bilateral suppression in jaw-closing muscle activity (Bratzlavsky, 1972; Yu *et al.*, 1973; Godaux and Desmedt, 1975; Ongerboor de Visser and Goor, 1976). These reflex studies document that neural pathways are available for short-latency lip-to-jaw interactions, but the reflex studies do not demonstrate the extent to which such interactions might operate throughout the course of speech movements.

If the jaw is able to compensate for perturbations in lip movement, it is not known to what extent the characteristics of such a response might vary with the positional or temporal requirements for compensation. The purpose of the present experiment was to perturb lower-lip movement prior to bilabial closure and to observe: (1) whether a compensatory response occurs, (2) if it does, whether it is exclusively performed by the upper lip or whether the jaw is able to compensate as well, and (3) whether the characteristics of any compensatory responses change relative to the timing of lip perturbation or to the jaw position at the onset of lip perturbation.

I. METHODS

Three normal-speaking young adults served as subjects. Subjects 1 and 2 were female. Subject 3 was a male.

Upper-lip, lower-lip, and jaw movements were transduced in the inferior–superior dimension with a strain gauge system (Muller and Abbs, 1979). The movement signals, audio from a dynamic microphone, and a marker indicating electrical stimulation were recorded on a Hewlett–Packard 3968A FM tape recorder. The tapes were later replayed and the signals were displayed with an optical oscillograph (Honeywell 1508 visicorder).[1]

Electrical stimulation was used to produce unexpected, involuntary depression of the lower lip. The electrical stimulation was delivered through two pairs of hooked-wire electrodes placed bilaterally in the vicinity of the depressor labii inferior muscle. The guidelines used for electrode placement are presented by Folkins (1978). The wires were inserted with separate 30-gauge, 1/2-in. hypodermic needles, with the two wires of a pair aligned approximately 20 mm apart. The teflon insulation was bared approximately 10 mm from the end of each 110-μm stainless-steel wire.

A Grass S4 stimulator was gated to produce 940-ms trains of 0.1-ms monophasic pulses at 65 Hz. The stimulator was attached to the electrodes through a Grass SIU5 stimulus isolation unit and two Grass CCU-1 constant current units. Current levels were adjusted so that large movements were achieved while keeping the current below levels at which subjects reported discomfort. The current to the left and right electrode pairs was adjusted separately until the involuntary lower-lip depression was bilaterally symmetric. Current levels ranged from 0.8 to 11.0 mA.

Both the force of muscle contraction from stimulation and the specific movements resulting from that muscle force will differ depending on a number of factors. For example, if the lip was already near a maximally lowered position, the stimulation might only continue to hold the lip down rather than producing additional lowering movement.

Figure 1 demonstrates a large involuntary lower-lip depression movement occurring when current was applied across both electrode pairs while the subject attempted to maintain a relaxed posture of the lips. A level of about 8.0 mm of depression was produced with a latency of approximately 200 ms. However, 6.3 mm of depression was reached within 100 ms. Table I shows that the three subjects reached from 5.3 to 7.7 mm of involuntary lower-lip depression within 100 ms

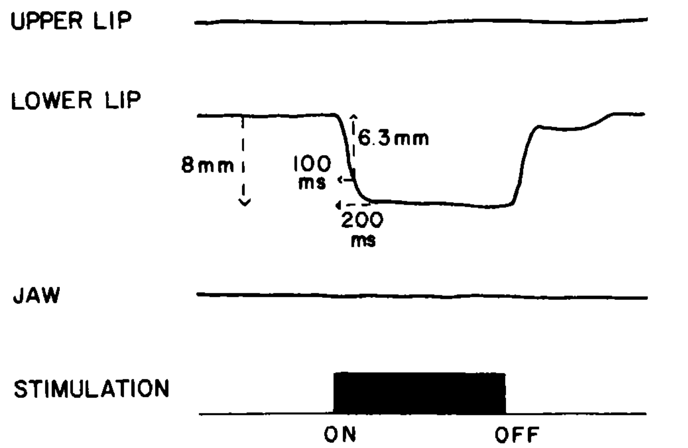

FIG. 1. An involuntary lower-lip depression movement produced by applying current across the bilateral electrode pairs in the vicinity of the depressor labii inferior muscles. The subject was attempting to keep the lip relaxed. Although 200 ms were required for the full 8 mm of involuntary movement, 6.3 mm of depression was reached within 100 ms.

TABLE I. Maximum displacement and time measurements of the involuntary lower-lip movements produced by stimulation. These measurements are illustrated in Fig. 1. Subjects attempted to keep the lip and jaw relaxed.

Subject	Maximum displacement (mm)	Time for maximum displacement (ms)	Displacement at 100 ms (mm)
1	8.3	200	6.3
2	13.0	300	7.7
3	7.3	180	5.3

after the onset of electrical stimulation. As illustrated in Fig. 1, stimulation of the lips at rest was not observed to influence jaw or upper-lip displacement.

Lip stimulation at rest was measured at the beginning and end of each experimental session and no sign of muscle fatigue from stimulation (Folkins, 1976) was observed.

All three subjects repeated tokens of [æp] 150 to 200 times with a pause of 2 to 4 s between syllables. Two to four rest periods were taken as requested by the subjects. Subjects 1 and 2 also repeated the task with the syllable [Ip]. Electrical stimulation of the lower lip was introduced during approximately one-third of the syllables. Syllables were chosen for lip stimulation at random except that stimulation was omitted from 80% of the instances when it would occur for two syllables in a row. This was done because only lip-stimulated syllables with a nonstimulated syllable occurring immediately preceding were used in data analysis.

A silent switch was activated by an experimenter when stimulation was to occur during the next syllable according to the randomization schedule. This experimenter stood outside of the sound-attenuated room (and out of the subject's view).[2] Stimulation was then triggered with a voice-activated timer to begin 100 to 400 ms following voice onset. During the recording sessions the duration of the delay was adjusted to various values to insure recording a number of syllables with stimulation beginning through a range of times prior to voice offset and bilabial closure. Only syllables with stimulation beginning within 40 to 500 ms prior to voice offset were included in the data analysis. This consisted of 20 to 33 tokens of [æp] for each subject, 22 tokens of [Ip] for subject 1, and six for subject 2.

The data were analyzed by comparing each stimulated syllable with the normal syllable immediately preceding it. This was done to take into account the normal variability in movement patterns inherent in multiple repetitions of an utterance. Movement patterns of adjacent syllables have been found to be more similar than those of separated syllables (Folkins and Abbs, 1975).

II. RESULTS

Magnitude of compensatory responses. Figure 2 shows a typical example of a normal and lip-stimulated syllable pair and illustrates many of the measurements made from the oscillographic displays. In this example stimulation began at a point with a jaw displacement of 18 mm at a time 200 ms prior to voice offset. Both jaw displacement and upper-lip displacement were measured from the resting position prior to movement to their position at the time of bilabial closure. The time of bilabial closure was defined operationally as the point when the upper lip first reached maximum inferior displacement.[3] In Fig. 2 the jaw was at 4.3-mm displacement when bilabial closure was reached in the normal syllable (point 1). In the lip-stimulated syllable the jaw moved up to 1.3 mm from the resting position by the time of bilabial closure (point 2). This represents a 3.0-mm increase in jaw movement in the syllable with stimulation. In a similar manner the upper lip increased movement for bilabial closure by 3.0 mm in the syllable with stimulation. Figure 3 is an example of a normal and stimulated pair for [Ip].

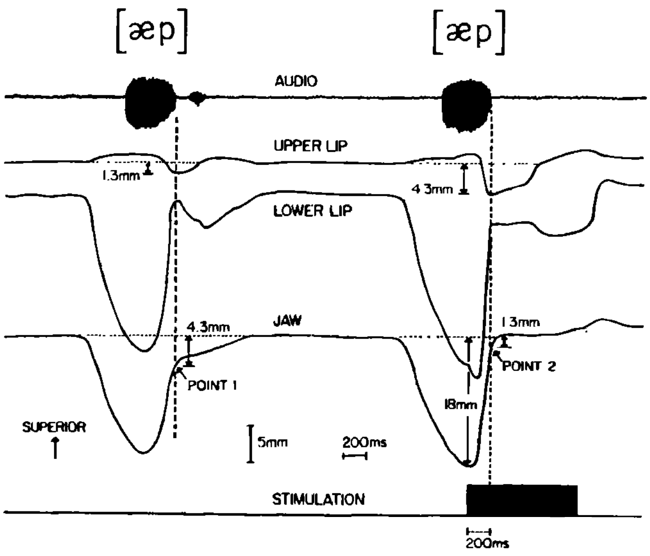

FIG. 2. An example of typical oscillographic records for a pair of [æp]s from subject 1. The syllable on the left is normal. In the syllable on the right electrical stimulation began 200 ms prior to voice offset. In the normal syllable the jaw was at 4.3-mm displacement from the rest position when bilabial closure was reached (point 1). In the syllable with lower-lip stimulation the jaw was at 1.3-mm displacement at bilabial closure (point 2). This is a 3.0-mm difference in jaw movement between syllables. The same measurements are illustrated for upper-lip displacement at bilabial closure. In this example stimulation began when the jaw was at 18.0-mm displacement.

The upper-lip and jaw displacements at bilabial closure were measured for all 104 syllable pairs included in the analysis. The means and standard deviations of these measurements are compared for the normal and lip-stimulated syllables in Fig. 4. A two-tailed t test for related pairs (Bruning and Kintz, 1968) was computed for each pair of normal and lip-stimulated syllables. All tests showed a significant change in displacement at $p < 0.05$.

Temporal effects on the magnitude of compensatory responses. Figure 5 is an example of the oscillographic display from a normal syllable and a syllable with

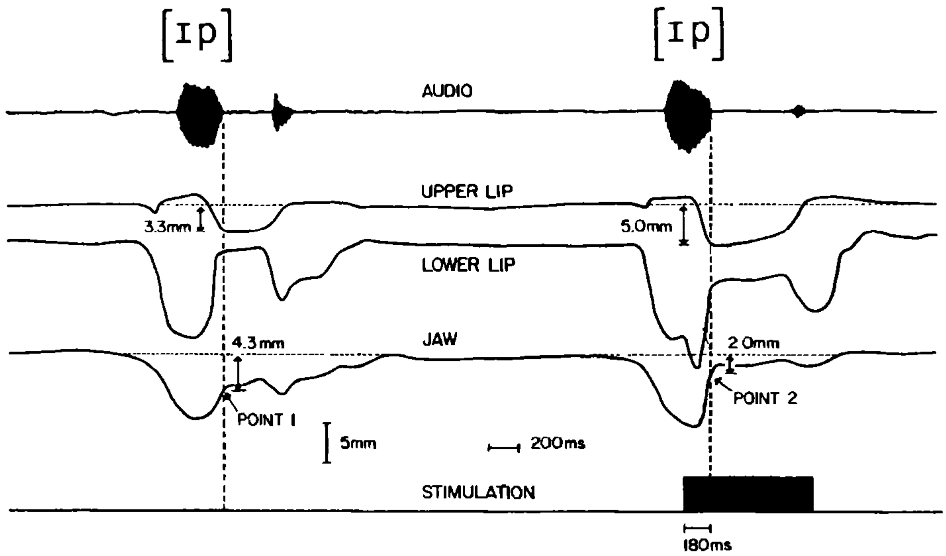

FIG. 3. An example of oscillographic records for a typical pair of [ɪp]s from subject 1. The syllable on the left is normal. In the syllable on the right, lower-lip stimulation was introduced 180 ms prior to bilabial closure. The measurements are the same as those described in Fig. 2.

lip stimulation only 40 ms prior to the offset of voicing. Jaw displacement at the time of bilabial closure is labeled point 1 for the normal syllable and point 2 for the syllable with lower-lip stimulation. The difference in jaw displacement between points 1 and 2 is 4.5 mm.

The jaw displacement at bilabial closure in each normal syllable has been subtracted from the jaw displacement for each following syllable with lower-lip stimulation. This was done to illustrate the effect of stimulation onset time on jaw compensation. These differences have been plotted as a function of the time between the onset of lower-lip stimulation and voice offset (Fig. 6). As the points are above the abscissa it appears that the jaw compensated for the stimulation by moving further. This was the case even when the stimulation preceded voice offset by as little as 40 to 100 ms. These data are from subject 3; however, the short-latency responses appear typical of the eight syllables with a 40- to 100-ms stimulation time present in the data from subjects 1 and 2.

In Fig. 7 the difference in upper-lip displacement between normal syllables and syllables with lip stimulation has been plotted as a function of the time between stimulation onset and voice offset. Again the data shown are from subject 3, but subjects 1 and 2 appeared to be similar. It appears that increases in upper-lip movement did not occur for the syllables with a short latency between stimulation onset and voice offset (and bilabial closure).[4] However, it should be emphasized that in the short-latency examples the stimulation produced a relatively small influence on the lower lip prior to bilabial closure. Small modifications in jaw movement alone should be adequate to counteract the lower-lip perturbation.

Jaw position and the magnitude of compensatory responses. Jaw displacement at bilabial closure was compared between normal syllables and syllables with lower-lip stimulation as a function of the position of the jaw at stimulation onset. As shown in Fig. 8 (from subject 2) the jaw produced larger compensatory movements in the syllables stimulated at the more open jaw positions. The correlations between magnitude of compensatory elevation movements and the jaw position at stimulation onset were 0.69, 0.55, and 0.42 for subjects 1, 2, and 3, respectively. All three correlations were significant ($p < 0.05$).

Timing of bilabial closure. In the 104 normal syllables bilabial closure was achieved within a range of −10 to +20 ms from the time of voice offset. In 70 of the syllables with lower-lip stimulation bilabial closure

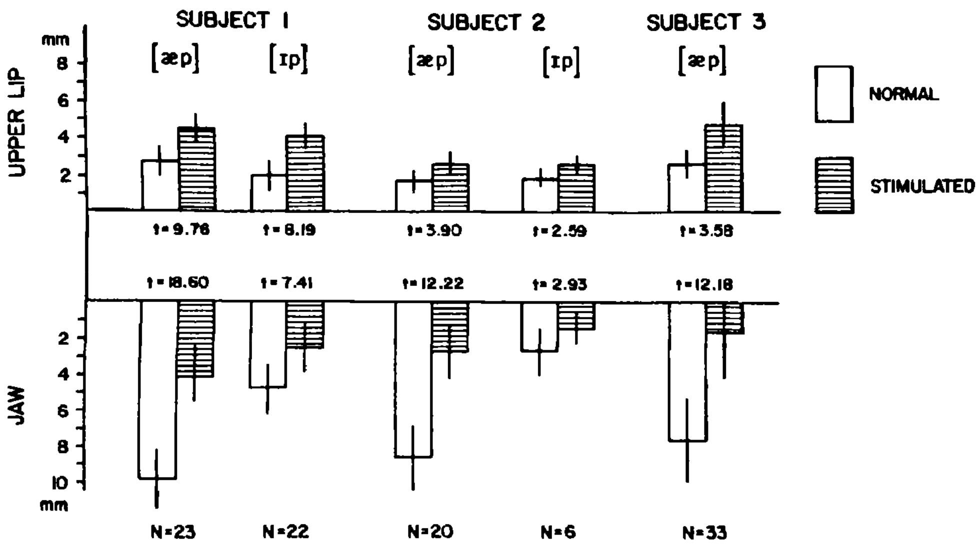

FIG. 4. Bar graph of mean upper-lip and jaw displacements at bilabial closure for the normal and lip-stimulated syllables. The vertical lines represent plus and minus one standard deviation. The jaw measurements are inverted to aid comparison to the oscillographic records. The t scores shown are from two-tailed t tests for related pairs. All t tests were significant ($p < 0.05$).

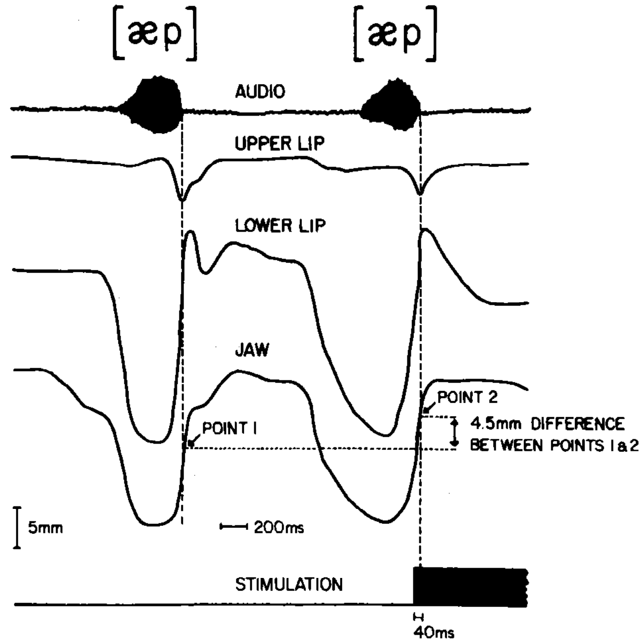

FIG. 5. An example of the oscillographic records for a normal syllable and a syllable with lower-lip stimulation beginning only 40 ms prior to the offset of voicing. Jaw displacement at bilabial closure is labeled point 1 for the normal syllable and point 2 for the syllable with lower-lip stimulation. These records are from subject 3.

appeared to have similar timing and it was reached within a range of −10 to +20 ms from the time of voice offset. In the other 34 syllables with lower-lip stimulation bilabial closure appeared to be delayed. In these syllables the mean delay in bilabial closure was 61 ms with a standard deviation of 33 ms.

The delays in bilabial closure were analyzed for a relationship to: (1) the timing of stimulation (and by inference the time available for producing compensatory responses), (2) the position of the jaw at stimulation onset, or (3) the size of the compensatory gestures produced. As reviewed in the next three paragraphs none of these analyses showed a significant relationship. Although these analyses do not lead to theories explaining why bilabial closure was delayed in some syllables and not in others, these findings do suggest that none of the descriptive data presented in previous sections were biased by inclusion of 34 syllables with delayed bilabial closure.

The mean time between stimulation onset and voice offset was 198 ms with a standard deviation of 99 ms in the syllables with a delay in bilabial closure. The mean stimulation-to-voice offset time was 226 ms with a standard deviation of 119 ms for the other 70 syllables with lip stimulation. Therefore it appears that the delays in bilabial closure did not tend to occur in syllables with an unusually short stimulation onset time. The extent of the delay in closure in each of the 34 syllables did not appear related to the time of stimulation ($r = 0.26$).

The delays in bilabial closure did not tend to occur in syllables with an especially large or small jaw displacement at stimulation onset. The mean jaw displacement at stimulation onset was 12.3 mm with a standard deviation of 3.7 mm in the 34 syllables with delayed bilabial closure. The mean displacement for the other 70 syllables with lip stimulation was 12.2 mm with a standard deviation of 4.8 mm. The extent of the delay in bilabial closure in the 34 syllables did not appear related to the jaw displacement at stimulation onset ($r = 0.00$).

The increases in jaw and upper-lip displacement did not appear to be appreciably larger in the syllable pairs with a delayed closure. The mean increase in jaw displacement following stimulation was 4.5 mm with a standard deviation of 2.3 mm in the 70 syllable pairs with normal timing for bilabial closure. The mean jaw-displacement increase was 5.6 mm with a standard deviation of 3.1 mm in the 34 syllables with delayed bilabial closure. The mean increase in upper-lip displacement was 1.3 mm with a standard deviation of 1.0 mm in the 70 syllable pairs with normal timing for bilabial closure and 1.3 mm with a standard deviation of 1.0 mm in the 70 syllable pairs with normal timing

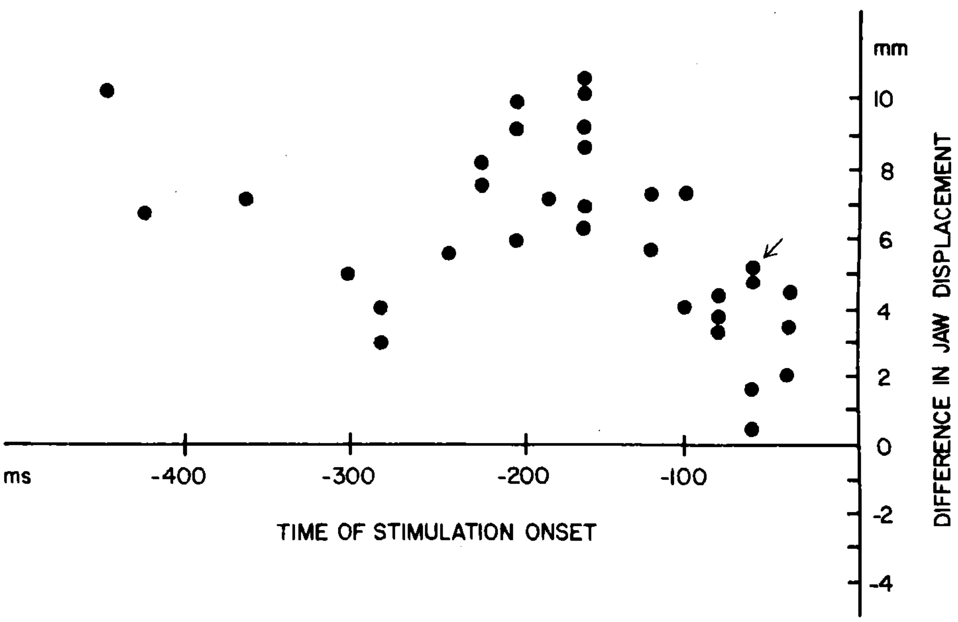

FIG. 6. Scatterplot of the difference in jaw displacement relative to the time of onset for lower-lip stimulation. The time of stimulation onset was measured in ms from the offset of voicing. The measurements of the difference in jaw displacement were obtained by subtracting the displacements at points 1 and 2 illustrated in Figs. 2, 3, and 5. These data are from subject 3. The arrow indicates the measurement from this subject's first syllable with stimulation.

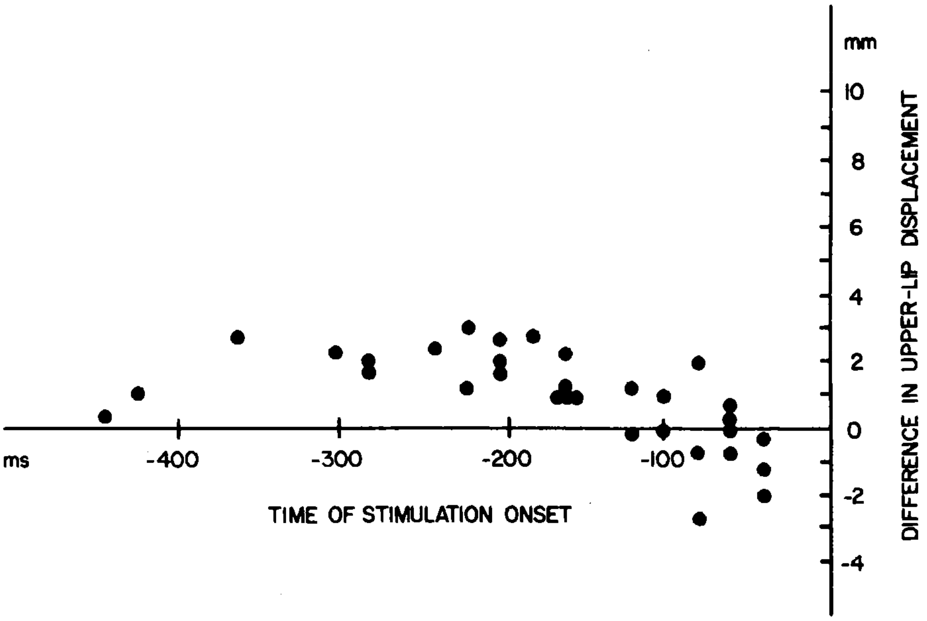

FIG. 7. Scatterplot of the difference in upper-lip displacement relative to the time of onset for lower-lip stimulation. The time of stimulation onset was measured in ms from the offset of voicing. The differences in upper-lip displacement were obtained by subtracting the upper-lip displacements at bilabial closure for each syllable pair. These data are from subject 3.

for bilabial closure and 1.3 mm with a standard deviation of 1.1 mm in the 34 syllables with delayed bilabial closure.

Duration and extent of jaw-closing movement. The duration and extent of the jaw-closing movement was measured in the 70 syllable pairs not showing a delayed bilabial closure. Jaw-closing duration was defined as the time between the onset of superior jaw movement for bilabial closure and the point at which bilabial closure was reached (as defined above). Jaw-closing extent is the distance moved by the jaw during the time defined as jaw-closing duration. The measurement defined as jaw-closing extent was suggested by an anonymous reviewer. It differs from all other movement measurements reported in this study which are displacements from rest position.

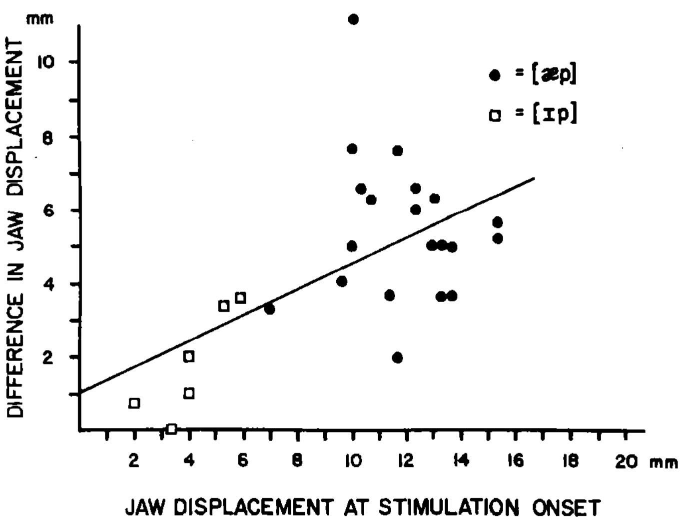

FIG. 8. Scatterplot of the difference in jaw displacement relative to the displacement of the jaw at the time of stimulation onset. The measurement of jaw displacement at stimulation onset is illustrated in Fig. 2. The difference in jaw displacement between syllables is the same measurement graphed in Fig. 6 and illustrated in Fig. 5. A linear regression line is shown through the data points ($r = 0.55$). These data are from subject 2.

The means and standard deviations for jaw-closing duration and extent are given in Table II. It appears that jaw-closing duration was very similar in the normal syllables and in the syllables with lower-lip stimulation and no delay in bilabial closure. Mean jaw-closing extent increased for all three subjects. Therefore the jaw-closing movements must have been faster in the syllables with lip stimulation than in the normal syllables if larger movements were produced in the same amount of time.

Timing of compensatory responses. Syllables with a large range in the timing of stimulation onset were included to assess whether the responses to stimulation were related temporally to the time of stimulation. In general it appeared that compensatory responses were manifest as increases in the displacement and velocity of jaw-closing movements rather than as separate, additional movements. When stimulation was initiated early in the syllable, there were no signs of a compensatory jaw-closing movement prior to the time when jaw-closing movements would be expected to begin in syllables without lower-lip stimulation.

The conclusion that compensatory responses were not temporally dependent on the time of stimulation onset is also supported by the data summarized in Table II. Table II shows that the mean duration of jaw-closing movements were similar in both the normal syllables and syllables with lower-lip stimulation. Therefore it does not appear that compensatory gestures in the syllables with early stimulation onset produced an early initiation of the jaw-closing movement.

Timing of voice offset. Folkins and Abbs (1975) observed that loading the jaw sometimes delayed the time of voice offset. The delay in that experiment ranged from a mean of 14 ms in one subject to 25 ms in another. The same comparison was made in the present experiment by measuring the duration of voicing for all syllables and finding the difference for each normal-stimulated pair. The duration of voicing increased in the syllables with lower-lip stimulation with a mean of

TABLE II. Mean values of jaw-closing duration and jaw-closing extent for the normal syllables and syllables with lower-lip stimulation. Standard deviations are shown in parentheses. Only syllables with no delay in bilabial closure were included in this analysis. The asterisks indicate statistically significant differences between means (two-tailed t test, $p < 0.05$). For these syllables it appears that stimulation produced appreciable differences in jaw-closing extent, but not jaw-closing duration.

Subject	N	Jaw-closing duration (ms) Normal	Stimulated	Jaw-closing extent (mm) Normal		Stimulated
1	31	124	119	6.2	*	9.8
		(37)	(31)	(3.6)		(4.4)
2	21	170	168	2.8	*	7.0
		(95)	(79)	(1.5)		(3.4)
3	18	93	102	7.5	*	12.0
		(24)	(37)	(1.8)		(2.1)
Total	70	130	130	5.4	*	9.5
		(65)	(57)	(3.3)		(4.7)

25, 21, and 17 ms for subjects 1, 2, and 3, respectively (two-tailed t tests for related measures were significant $p < 0.05$ for subjects 1 and 3).[5] As in the previous experiment it is not clear whether the increased voicing duration was due to an active laryngeal response to perturbation or to a delay in the buildup of intraoral air pressure. Using voice offset in the calculation of stimulation onset time may have produced a discrepancy (perhaps up to 25 ms) in the stimulation onset measures relative to the time that voice offset would have occurred if the lip had remained unperturbed. However, because voice duration only changed by such small amounts, it appears that lower-lip stimulation did not delay voice offset to an extent that would have an appreciable effect on the movements measured. Therefore the usage of voice offset time in defining the timing of stimulation onset appears justified.

Changes in compensatory responses during the experiment. The arrow in Fig. 6 indicates the measurement produced by subject 3 the first time he was given lower-lip stimulation during syllable production. For this token it appears that a large compensatory jaw movement was produced within a relatively short time interval (60 ms). Therefore it does not appear that subject 3 learned a compensatory strategy only after the first few times he experienced stimulation. He compensated for stimulation on the first occurrence. Stimulation in the first syllables for subjects 1 and 2 was timed too late for inclusion in the data.

In general no systematic changes in the character of compensatory responses in the upper lip or jaw were observed to occur as the experimental sessions progressed. That is, no modifications in compensatory gestures were noticed that might have been learned after the subject's first few productions with lower-lip perturbation.

III. DISCUSSION

Effect of stimulation timing on compensatory responses. In the study of cat locomotion it has been observed that both the direction and timing of compensatory responses will vary depending on the timing of a perturbation relative to the step cycle (Forssberg *et al.*, 1975, 1977, 1980; Forssberg, 1979). In the present experiment syllables with large range in the timing of stimulation onset were deliberately included in the data analysis to assess whether compensation varied with the time of stimulation. No compensatory responses were observed at consistent latencies following stimulation onset. Rather, the compensation occurred at times that made them appear as an increase in the magnitude of the closing movements. This is illustrated in Figs. 2 and 3. As in cat locomotion the compensatory responses must have involved more than simply triggering a low-level reflex with a relatively constant latency. Although reflex arcs are undoubtedly involved, the motor system must somehow adjust the timing of compensatory responses so that they are restricted relative to the time course of the ongoing movement and not to the timing of the external stimulus.

Compensatory responses from the jaw were evident in the shortest time intervals analyzed, 40 ms. The size of the jaw compensations varied in relation to the onset time of lower-lip stimulation and jaw position at stimulation onset. When the time available for a compensation was decreased, so was the size of the compensation necessary. Therefore minimum latencies required for eliciting the compensatory effects could not be measured.

There did not appear to be a noticeable change in response characteristics across the latencies of 100 to 150 ms that might be expected for a voluntary reaction-time response (McClean and Cooker, 1980). Even if processes similar to voluntary reaction-time responses were involved in some aspects of the long latency compensatory movements, the issue-important finding is that subjects were able to make appropriate compensatory responses.

A reviewer of this paper suggested that the jaw-closing muscles may have been inadvertently stimulated when the current was applied to the lower lip. Such stimulation might produce the increased jaw-closing movements seen in the results. This possibility is unlikely because: (1) No superior movement of the jaw was seen when stimulation of the lower lip was produced at rest as illustrated in Fig. 1. This is not surprising as we have not been able to produce a measurable amount of jaw-closing movement from subpainful current levels unless the electrodes for stimulation are within or in very close proximity to a jaw-closing muscle. (2) Direct electrical stimulation produces movement with a consistent poststimulation latency. A consistent post-stimulation latency was not observed for the superiorly directed jaw-closing movements.

Comparison between lip perturbation and jaw perturbation. Although both the jaw and upper lip were able to compensate for the perturbations in lower-lip movement, bilabial closure was delayed in 32% of the syllables with lower-lip stimulation. In the Folkins and Abbs (1975) study in which the jaw was loaded and the lips compensated, bilabial closure did not appear to be delayed relative to voice offset in any of the jaw-loaded syllables. This may reflect a true difference between the lip and jaw relative to the consistency with which compensatory gestures can be produced. Or alternatively, it may reflect differences between the paradigms used in the two studies.

In the Folkins and Abbs (1975) study the perturbation was variable in that the jaw was stopped or retarded at different positions. In the present study lower-lip perturbation was not only variable, but lip movement was reversed in direction rather than just stopped or retarded. Furthermore, in the present paradigm the influence of muscle stimulation might have varied substantially depending on the peripheral conditions of the lip. At the time of stimulation the length of the stimulated muscles, the velocity of muscle contraction, the amount of background activity in the stimulated muscles, and the interactions with other lip muscle tissue (among other factors) may have influenced the effects of stimulation on lower-lip movement. These differences in paradigms may have made compensations in the present study more difficult to achieve with typical timing characteristics than in the jaw-loading paradigm.

There are a number of additional differences between the present study and the jaw-loading experiment. For example, unlike the Folkins and Abbs (1975) study, in the present experiment it was possible for the perturbed structure (i.e., the lower lip) to compensate as well as other structures. If this did happen, the results of Kennedy (1977), Bizzi *et al.* (1978), and Tatton and Bawa (1979) suggest that the autogenic compensatory adjustments from the perturbed structure would be relatively small. Another difference between paradigms is that in the present study the electrical stimulation may have activated sensory nerve fibers in the lower lip. Such activation might have signaled a perturbation, masked sensory information from the lip, or had any number of other effects.

In Fig. 8 it can be seen that the compensatory gestures were larger when stimulation occurred at lower jaw positions. Furthermore, in both Figs. 4 and 8 it appears that compensatory jaw movements were larger for [æp] than [Ip]. In the Folkins and Abbs (1975) experiment it was also observed that the compensatory gestures were larger when the jaw was loaded at more open positions. However, in the jaw-loading experiments the perturbation was obviously different at the different jaw positions. In the present experiment it is also possible that at the more open jaw positions the stimulation had a larger effect on the lower lip and required larger compensations. However, another possibility is that the subjects compensated predominantly with the jaw at more open positions and relied more on the lower-lip muscles to overcome the perturbation at the more closed positions. The lips move further for the more open gestures and it seems logical that larger lip-closing movements might be more impaired by stimulation than the smaller lip-closing movements. Therefore the subjects used more jaw movement in this circumstance.

In conclusion, it appears that the upper lip and jaw are able to make compensatory movements to aid bilabial closure following unexpected perturbation of the lower lip. Additional research may help contrast responses to lip perturbation with the responses to jaw loading reported by Folkins and Abbs (1975). Furthermore, it may be that interactions between the lips and jaw may be different for bilabial closing, bilabial opening, labiodental closing, and lip-rounding gestures.

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[1]Originally it was planned to measure electromyographic activity from a number of jaw and lip muscles; however, in pilot work it was found that a large stimulus artifact from electrical stimulation obscures the action potentials and makes the electromyographic data unusable. During the experiment electromyographic activity was recorded from medial pterygoid in one subject, but stimulus artifact still obliterated the electromyographic signals in spite of the distance between the stimulation electrodes and the medial pterygoid muscle.

[2]The jaw-movement tracings were analyzed for evidence that the subjects anticipated stimulation. Jaw displacement was measured at the time of stimulation onset and compared to jaw displacement at the same time (preceding voice offset) in the normal syllable immediately prior to each syllable with labial stimulation. The differences between means in this analysis were 0.1, 0.0, and 0.3 mm for the three subjects. This suggests that the subjects did not move the jaw to a novel position prior to the onset of stimulation.

[3]This estimate may be slightly later than the time when the lips come into contact due to the compressibility of the labial tissue.

[4]The negative values at short latencies appear to be due to the normal syllable-to-syllable variability that would occur without stimulation.

[5]Voicing duration was also analyzed separately for the syllables with and without a delay in the timing of bilabial closure. For the syllable pairs with no delay in bilabial closure the mean increases in voicing duration for subjects 1, 2, and 3 were 8 ms (standard deviation- 36 ms), 32 ms (standard deviation =98 ms), and 17 ms (standard deviation=39 ms). For the syllable pairs with a delay in bilabial closure the mean increases in voicing duration were 30 ms (standard deviation = 47 ms), -12 ms (standard deviation = 36 ms), and 17 ms (standard deviation = 32 ms). None of these changes in voicing duration were statistically significant with a two-tailed t test for related pairs.

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