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RESEARCH ARTICLE

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Task-specific sensorimotor interactions in speech production

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Abstract Speaking involves the activity of multiple muscles moving many parts (articulators) of the vocal tract. In previous studies, it has been shown that mechanical perturbation delivered to one moving speech articulator, such as the lower lip or jaw, results in compensatory responses in the perturbed and other non-perturbed articulators, but not in articulators that are uninvolved in the specific speech sound being produced. These observations suggest that the speech motor control system may be organized in a task-specific manner. However, previous studies have not used the appropriate controls to address the mechanism by which this task-specific organization is achieved. A lack of response in a non-perturbed articulator may simply reflect the fact that the muscles examined were not active. Alternatively, there may be a specific gating of somatic sensory signals due to task requirements. The present study was designed to address the nature of the underlying sensorimotor organization. Unanticipated mechanical loads were applied to the upper lip during the “p” in “apa” and “f” in “afa” in six subjects. Both lips are used to produce “p”, while only the lower lip is used for “f”. For “apa”, both upper lip and lower lip responses were observed following upper lip perturbation. For “afa”, no upper lip or lower lip responses were observed following the upper lip perturbation. The differential response of the lower lip, which was phasically active during both speech tasks, indicates that the neural organization of these two speech tasks differs not only in terms of the different muscles used to produce the different movements, but also in terms of the sensorimotor interactions within and across the two lips.

Keywords Speech motor control · Sensorimotor · Task-dependent · Speech movements

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Introduction

Research in speech motor control has provided evidence for the importance of sensorimotor interactions in the coordination of speech movements. Using unanticipated perturbation of a single articulator, such as the jaw or lower lip during speaking, kinematic and EMG changes in the perturbed articulator, as well as non-perturbed articulators, have been observed. Perturbations to the lower lip during bilabial closure for “aba” result in rapid compensatory changes in both the lower lip and upper lip, in the form of increased EMG activity and movement displacements, durations and velocities (Abbs and Gracco 1984; Gracco and Abbs 1985). Such responses, occurring in less than a reaction time, indicate that somatic sensory information from orofacial structures can rapidly access orofacial motor output.

It appears, further, that the observed interaction between the upper and lower lips is not merely a generalized response to the load, but, rather, a response that is specific to the task. For example, in a task where only the lower lip is active (for “f”), lower lip or jaw loads produce no upper lip response (Abbs et al. 1984; Abbs et al. 1985; Shaiman 1989). In a task in which the tongue is active but not the upper lip, a jaw load produces only tongue and lower lip changes (Kelso et al. 1984). These results have been used to suggest that, for a given speech motor behavior, the sensorimotor organization among the various articulators is adjusted for the specific task. Such task specificity has been demonstrated in the complex movements associated with postural adjustments (Cordo and Nashner 1982; Marsden et al. 1981; Nashner and Cordo 1981), locomotion (Forssberg et al. 1975; Quintern et al. 1985) and hand movements (Cole et al. 1984; Traub et al. 1980).

However, the previous speech perturbation results used to implicate a task-specific organization have a significant weakness that limits the ability to interpret the results unambiguously. In the case of a lower lip perturbation during "afa", the motor neurons for upper lip muscles may not be activated enough to elicit a response resulting from the somatic sensory input from the lower lip load. The underlying mechanism for producing a specific speech sound could be one in which only the appropriate motor neuron pools are activated, reflecting a predominantly motor organization. Alternatively, the motor control mechanism may include specific modulation or gating of somatic sensory information that varies with the particular speech sound being produced, reflecting a sensorimotor organization.

To address this issue, responses should be examined during tasks in which the non-perturbed structure is phasically active, thereby indicating motor neuron activation. In the current study we examined the task-dependent nature of two speech utterances, in which the non-perturbed structure was phasically active for both tasks. More specifically, lower lip responses to upper lip perturbations during "apa" and "afa" were compared. Since the lower lip is phasically active during elevation for both tasks, if there is a task-dependent sensorimotor organization, significant lower lip adjustments should be observed in order to compensate for upper lip perturbations during "apa", with no compensatory responses to upper lip perturbations during "afa".

Materials and methods

Subjects

Subjects were six normal adult females, ranging in age from 18 to 30 years. Only female subjects were used in order to minimize potential load effect differences and maintain consistency with previous speech perturbation studies (e.g., Abbs et al. 1985; Gracco and Abbs 1985; Shaiman 1989). Subjects reported no neurological, speech or hearing difficulties. Subjects were naive as to the objectives of the experiment and to the procedures used in speech motor control research.

Perturbation characteristics

Unanticipated perturbations were applied to the upper lip in a superior direction, using a DC brushless torque motor (Aeroflex No. TQ34 W-12) (cf. Abbs and Gracco 1984; Gracco and Abbs 1985). Rotation of the torque motor sector arm was transmitted to the upper lip using a stainless steel wire and low friction lever, attached to a rectangular paddle (with a surface area of 1.3 cm) resting midline on the upper lip. Strain gauges bonded to the sector arm were used to transduce the force applied to the upper lip, with resolution of less than 0.5 g. The torque motor operated under force feedback control, following speech movements with constant, non-elastic tracking loads of 3–6 g, and thus not interfering with normal speech movements, based on experimenter observation (cf. Abbs and Gracco 1984) and subject report (cf. Gracco and Abbs 1985). The torque motor delivered superiorly directed loads to the upper lip, with a force magnitude of 0.4 N, a rise time of 15 ms, and a load duration of 250 ms. These load characteristics were chosen to ensure that the resulting displacements, velocities and accelerations were within the range of normal lip movements for speech (Gracco 1994; Hirose et al. 1982; Sussman et al. 1973). Perturbations were randomly introduced on 15% of the trials to minimize adaptation to or anticipation of the perturbation (Abbs and Gracco 1984). The target interval for the loads was a 100-ms interval centered on the onset of orbicularis oris inferior electromyographic activity associated with lower lip elevation for "p" and "f" (cf. Abbs and Gracco 1984; Shaiman 1989).

Movement transduction

Inferior-superior movement of the upper lip was transduced using the rotational variable differential transformer that was part of the torque motor system. The design of the sector arm of the torque motor resulted in linear translation of the wire that was proportional to the rotation of the torque motor shaft, providing a resolution of at least 0.3 mm (cf. Abbs and Gracco 1984).

Inferior-superior movement of the lower lip was transduced using a lightweight, head-mounted cantilever beam strain gauge transduction system (Barlow et al. 1983). Jaw movement was eliminated by having subjects bite on custom-fitted dental blocks (10 mm between the central incisors) throughout the experiment.[1]

Movement signals were digitally filtered (forward and backward for zero phase lag) prior to analysis, using a four-pole, 20-Hz low-pass Butterworth-like filter implementation in software.

Electromyography

Electromyographic (EMG) activity was recorded from two lower lip elevator muscles, orbicularis oris inferior (OOI) and mentalis (MTL), and an upper lip depressor, orbicularis oris superior (OOS), using bipolar, hooked-wire electrodes. Electrodes were constructed of 70-μm enamel-coated copper wire with 1–2 mm of the insulation removed from the hooked end. Each wire of the bipolar pair was inserted separately, approximately 4 mm apart, using a 30-gauge hypodermic needle. Electrode placements were determined by previous human cadaveric studies (Kennedy and Abbs 1979) and palpation. Verification gestures were used to ensure that the sampled muscles contributed to the speech motions associated with upper lip lowering and lower lip raising (e.g., O'Dwyer et al. 1981). EMG signals were preamplified in the pass band of 22 Hz to 22 kHz, with additional amplification in the pass band of 50 Hz to 2.5 kHz prior to computer digitization.

Movement tasks

Subjects were instructed to take a breath and sustain the vowel "a" (/æ/, phonetically). Upon hearing a tone, they were to produce the sound "pa" or "fa" as quickly as possible, and then resume the sustained "a". Subjects were not informed of the possibility of lip perturbations. Counterbalanced groups of subjects began with either "apa" or "afa". 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.

[1] Folkins and Zimmermann (1981) previously demonstrated that the phasic pattern of EMG activity for jaw closing muscles does not change when a bite block is in place. This suggests that the presence of a bite block does not eliminate normal coordinative patterns.

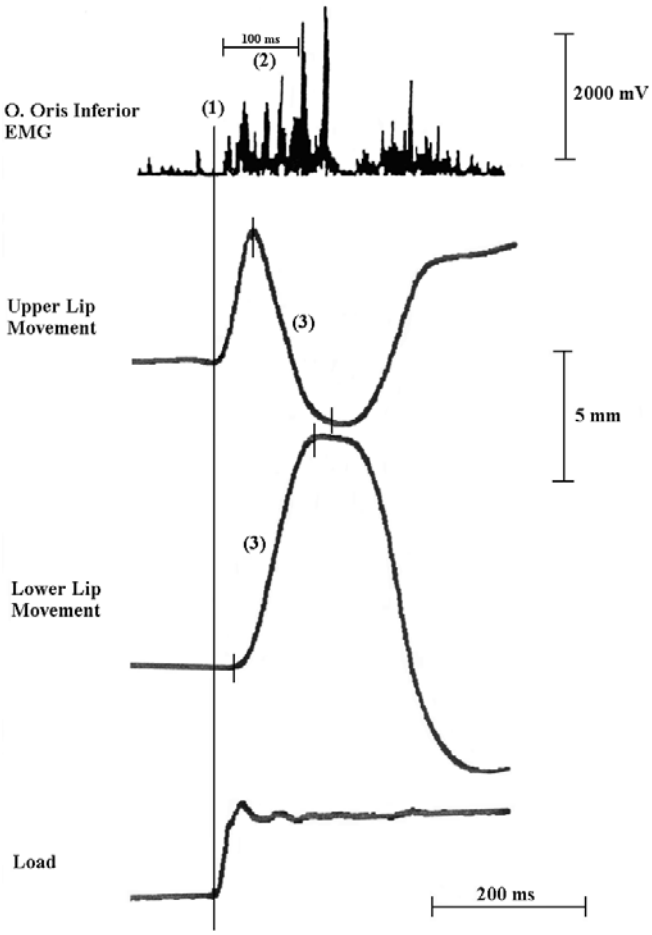

Fig. 1 Movement and EMG events used to derive the measured variables: *(1)* load onset time; *(2)* EMG area; and *(3)* movement displacements, velocities and durations

Data acquisition and analysis

All signals were digitized (12-bit resolution) online. Movement and force signals were digitized at 600 samples/s; EMG signals were digitized at 3,000 samples/s. Upper and lower lip displacement onsets and offsets were defined algorithmically in software using 5% of peak closing velocity as the criterion. EMG onsets were manually indexed, using two standard deviations above baseline for at least 20 ms as the criterion.

The following measures, illustrated in Fig. 1, were obtained: (1) time of load onset in relation to the onset of the phasic burst in OOI EMG activity; (2) area under the curve for the first 100 ms of the phasic EMG bursts (rectified and smoothed) for all muscles; and (3) upper lip and lower lip displacements, from onset to offset, and associated peak velocities and movement durations. Only the control-load pairs in which the time of load onset occurred within ±50 ms of the onset of OOI EMG activity were subjected to statistical analysis.

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 ("apa" vs "afa") and condition (control vs 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, two-tailed paired *t*-tests were performed for each individual subject. The alpha level for all statistical procedures was $P<0.01$.

Results

A total of 373 perturbations were introduced in the target interval during productions of "apa" across the six subjects, while 389 perturbations were introduced during productions of "afa". Both lower lip and upper lip compensatory adjustments were evident in the movement and EMG responses to perturbations of the upper lip during "apa". Conversely, lower and upper lip compensatory responses were noticeably absent during productions of "afa".

Kinematic responses

Figure 2 illustrates a control-load response for one subject's productions of "apa" and "afa". Upper lip perturbations during "apa" resulted in increased displacement in both lower lip and upper lip movement. These displacement changes were achieved through a combina-

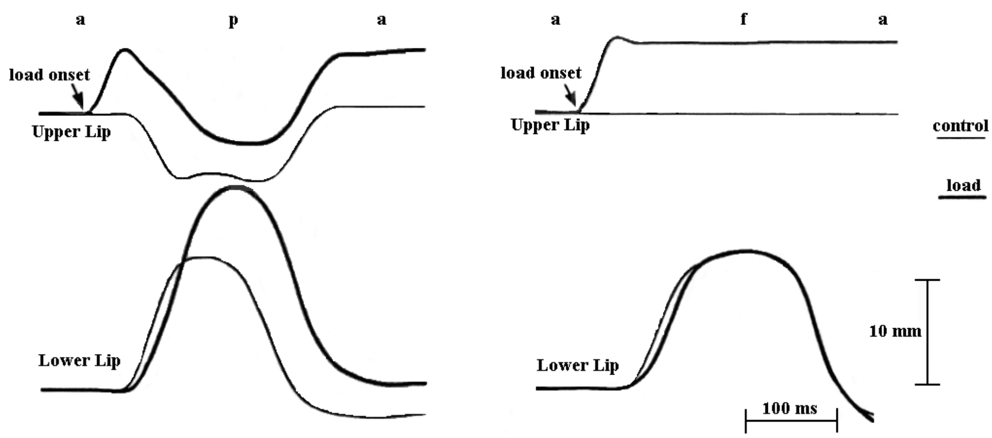

Fig. 2 Control-load pair of upper and lower lip displacement for the production of "apa" and "afa". *Thick lines* represent load trials

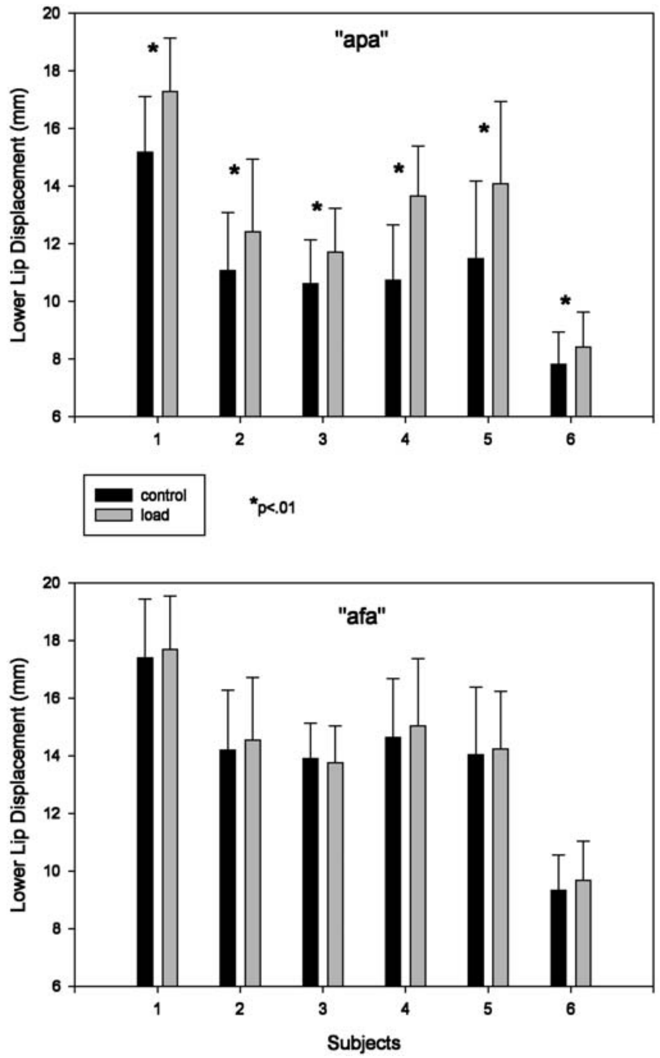

Fig. 3 Mean lower lip displacements (and standard deviations) for control and load trials of the six subjects' productions of "apa" (*top*) and "afa" (*bottom*)

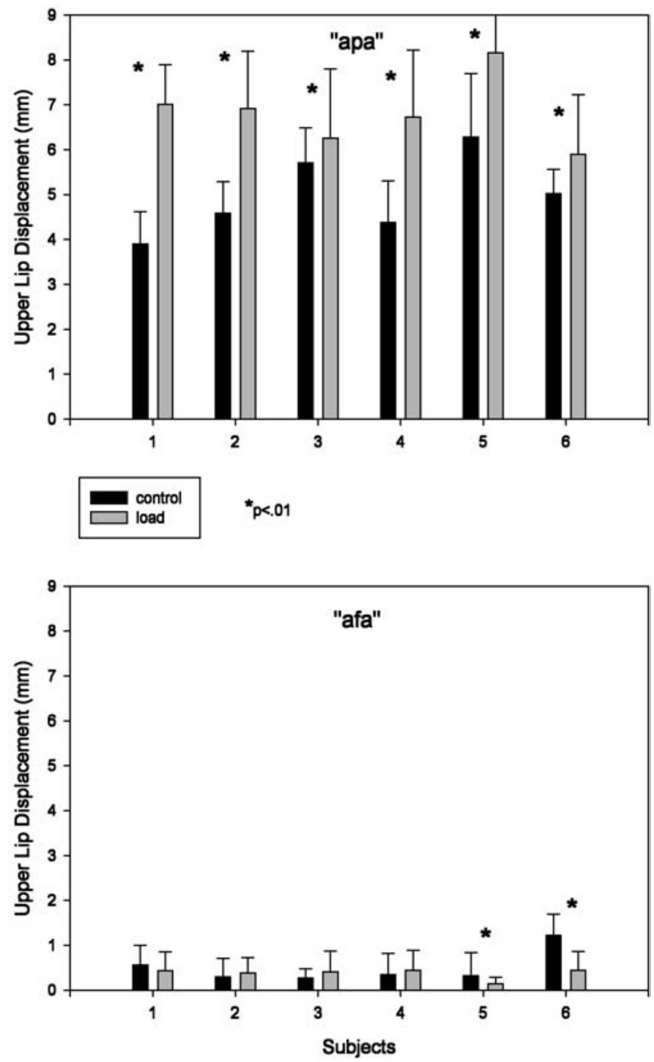

Fig. 4 Mean upper lip displacements (and standard deviations) for control and load trials of the six subjects' productions of "apa" (*top*) and "afa" (*bottom*)

tion of movement duration and peak velocity adjustments, similar to those observed by Gracco and Abbs (1985). In contrast, during the production of "afa", upper lip perturbations resulted in no movement changes in either the lower lip or upper lip.

Analysis of lower lip displacements indicated an utterance by condition interaction ($F_{(1,5)}$=18.74, P=0.008). Lower lip displacements increased significantly ($F_{(1,5)}$=50.02, P<0.001) for perturbed trials for "apa", in which both the upper lip and lower lip are involved. Conversely, lower lip displacements showed no significant difference ($F_{(1,5)}$=0.90, P>0.05) between control and load trials for "afa", in which the upper lip is not involved. Figure 3 illustrates the lower lip displacement findings for all six subjects. This indicates that, for each individual subject, lower lip displacement for load trials increased significantly relative to control trials during the production of "apa". Conversely, during production of "afa", load-control differences in lower lip displacement were non-significant for all subjects. The utterance by condition interactions were non-significant for both lower lip peak velocity ($F_{(1,5)}$=2.93, P=0.148) and movement duration ($F_{(1,5)}$=5.94, P=0.059).

A significant utterance by condition interaction ($F_{(1,5)}$=27.50, P<0.004) was also noted for upper lip displacement. Upper lip displacement increased significantly ($F_{(1,5)}$=50.02, P<0.001) for perturbed trials during the production of "apa", while changes were non-significant ($F_{(1,5)}$=0.903, P>0.05) during the production of "afa". All individual subject responses were consistent with this pattern, as shown in Fig. 4, with two subjects (S5 and S6) actually showing a decrease in upper lip displacement during load trials of "afa". While there was no utterance by condition interaction for upper lip peak velocity ($F_{(1,5)}$=0.64, P=0.461), the upper lip dura-

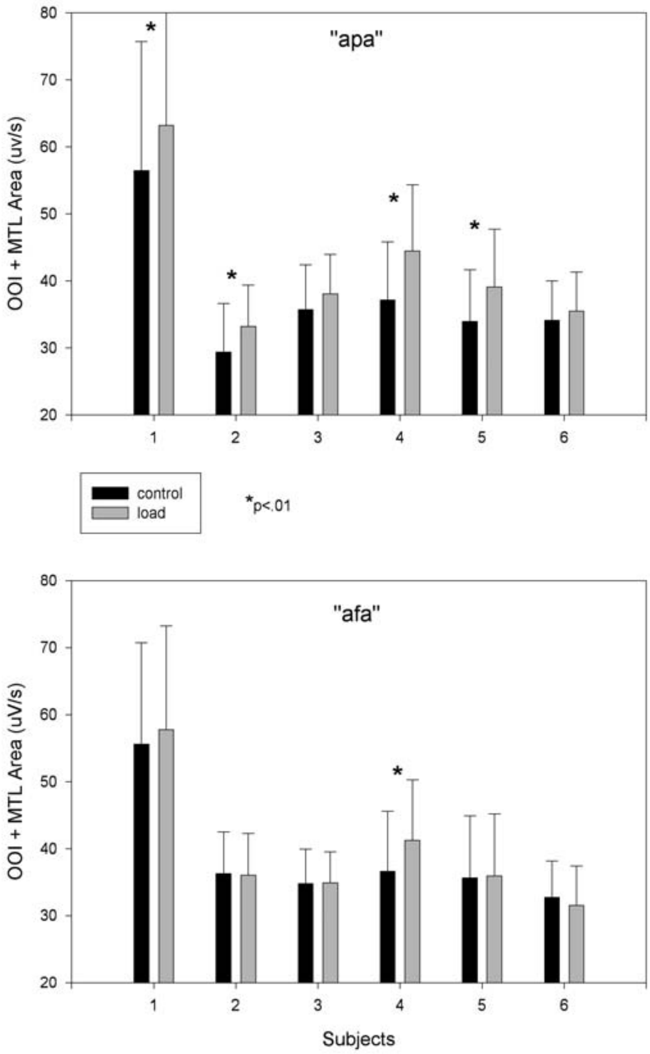

Fig. 5 Mean lower lip EMG areas (and standard deviations) for control and load trials of the six subjects' productions of "apa" (*top*) and "afa" (*bottom*)

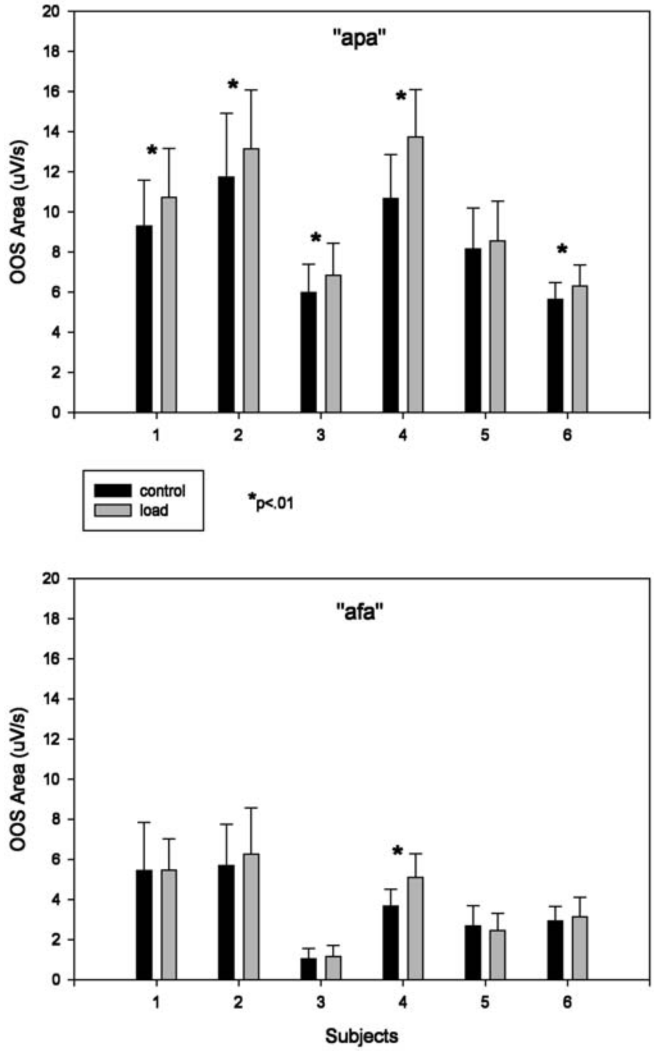

Fig. 6 Mean upper lip EMG areas (and standard deviations) for control and load trials of the six subjects' productions of "apa" (*top*) and "afa" (*bottom*)

tion interaction was significant ($F_{(1,5)}$=32.81, P=0.0023). Analyses indicated that upper lip movement duration increased significantly ($F_{(1,5)}$=31.84, P<0.01) for perturbed trials during the production of "apa", while changes were non-significant ($F_{(1,5)}$=7.17, P>0.01) during the production of "afa".

Electromyographic responses

Electromyographic responses were consistent with the kinematic findings. That is, both lower lip and upper lip musculature demonstrated increased activity to upper lip perturbations during the production of "apa", but not during "afa". Lower lip findings are based on analysis of the combined OOI and MTL activity. The combined activity is presented because this muscle pair is synergistic in elevating the lower lip (Folkins and Abbs 1976).

Analysis of group data for OOI+MTL indicated a significant ($F_{(1,5)}$=54.31, P<0.0008) utterance by condition interaction. The combined muscular activity of lower lip elevators exhibited a significant increase ($F_{(1,5)}$=175.96, P<0.001) to perturbations during the production of "apa", but not during "afa" ($F_{(1,5)}$=8.082, P>0.01). Individual subjects, as illustrated in Fig. 5, generally followed this pattern: three of the six subjects evidenced significant EMG increases during "apa", but not "afa"; two subjects showed no significant electromyographic increase for either "apa" or "afa"; one subject showed increased EMG activity during both "apa" and "afa".

Similarly, analysis of group data for OOS (an upper lip depressor) indicated a significant ($F_{(1,5)}$=25.30, P<0.005) utterance by condition interaction. OOS activity increased significantly ($F_{(1,5)}$=18.83, P<0.01) to perturbations during the production of "apa", but not during the production of "afa" ($F_{(1,5)}$=1.44, P>0.25). Figure 6 demonstrates that individual subjects were consistent in this pattern, with the exception of S4, who also exhibited increased OOS activity during "afa", and S5, who demonstrated no increases in OOS activity across either utterance.

Discussion

In order to place these results in the appropriate context, it is first helpful to consider something about the control of speech movements from a conceptual level. The presence of a compensatory response in the upper and lower lips to upper lip perturbation during "p" supports and extends previous speech perturbation studies. The common feature of these studies is that the observed compensation is distributed to the perturbed as well as the unperturbed speech articulators as long as they are participating in the particular speech task (Abbs and Gracco 1984; Folkins and Abbs 1975; Gracco and Abbs 1985, 1989; Shaiman 1989; Kelso et al. 1984; Kollia et al. 1992; Munhall et al. 1994). Conceptually, this is an important characteristic of the speech motor control system (and other functional multijoint or multiarticulate behaviors), demonstrating that speech motor actions are planned, organized and controlled at a goal level rather than at the level of individual muscles or single articulators.

At a physiological level, other considerations are reflected in the present results. Similar to previous studies, the presence of the load never disrupted the speech motor task. Additionally, the compensatory responses that were observed were not time locked to the onset of the load but were incorporated into the ongoing voluntary motor task (Abbs and Gracco 1984; Gracco and Abbs 1985). Moreover, the fact that the responses included in the analysis were limited to those in which the load was applied within a 100-ms interval centered on the onset of the voluntary EMG activity means that cortical motor potentials would be well underway. It seems reasonable to conclude, therefore, that the observed responses reflect the real-time operation of the speech motor control system. These responses, then, do not solely represent obligatory reflexes or exclusively voluntary adjustments but a set of sensorimotor interactions in which reflex pathways contribute to ongoing modulation of voluntary motor commands.

The observed compensation reflects the sensorimotor link between orofacial somatic sensory receptors and neural control signals associated with the "motor plan" allowing rapid adjustments to ongoing motor actions similar to those observed in studies of postural reactions and adjustments in precision grip (Cordo and Nashner 1982; Marsden et al. 1981; Nashner and Cordo 1981; Flanagan et al. 1993; Flanagan and Wing 1993, 1995). In the present study, the lower lip is the prime oral articulator for "f" and the lower lip elevates to contact the upper teeth. For "p", the upper and lower lips contribute cooperatively to close the oral end of the vocal tract. The results suggest that upper lip afferences are distributed to both upper and lower lip motor neurons for a consonant sound involving both lips ("p"). For "f", the upper lip afferences due to the application of a load were not distributed to the lower lip. The lack of response in the face of activation of lower lip muscles for both consonants indicates that there was a state-dependent modulation of upper lip somatic afferents accompanying the two different speech sounds. It is not clear from these results, however, whether this modulation was due to presynaptic inhibition of upper lip afferents (a gating) or the lack of postsynaptic facilitation of upper lip afferents onto lower lip motor neurons.

These findings are consistent with the construct that groupings of muscles or structures may be temporarily and flexibly marshaled together and constrained as a task-specific, functional unit. Such an organization has been termed a "coordinative structure" or "functional synergy" (Bernstein 1967; Fowler et al. 1980; Kelso et al. 1983). Previous studies have suggested that compensation is a characteristic of such functional groupings, with compensatory interactions being representative of normally occurring interactions among articulators in non-perturbed speech (Folkins and Linville 1983; Kelso et al. 1984). The current findings are consistent with the operation of coordinative structures, in that the sensorimotor organization among the various articulators is flexibly adjusted based on the specific task requirements (e.g., Kelso et al. 1984; Munhall et al. 1994).

An observation should be made about the differences in activation level of the upper lip for the two speech sounds. While the upper lip muscles were active for "f", they were significantly less active than for "p". It is not clear how this difference in activation levels would affect the sensory input resulting from the load. Presumably it would result in a variety of differences between the effects of the load for the two consonant sounds. However, it is known that passive movement can have substantial effects on reflex excitability of spinal and supraspinal pathways (Brooke et al. 1999; Lewis et al. 2001) and passive movement of a structure can disrupt interlimb coordination even when the passively moved structure is not involved in the behavior (Swinnen et al. 1995).

A final observation should be made regarding subject variability. In reviewing the individual subject data, responses were, in general, consistent with the findings of the group statistical analyses. However, there were some discrepancies between the kinematic and EMG data for individual speakers. For example, two subjects (S3 and S6) demonstrated no significant change in lower lip EMG activity to upper lip perturbations for "apa" despite significant increases in lower lip displacements. Similarly, one subject (S4) demonstrated a significant increase in lower lip EMG activity to perturbations for "afa", yet showed no significant change in lower lip displacement. Such discrepancies are likely a reflection of a number of factors. First, the perioral muscles are interdigitated, and the ability to map EMG to a specific muscle is problematic. The activity recorded reflects not only the muscle of interest, but also any interdigitated fibers from other muscles that may be synergistic or antagonistic to the muscle of interest. Second, the orientation and architecture of the muscles make their actions biomechanically complex. As such, identifying a perioral muscle as being associated with a particular action or movement direction is a simplification. Muscle activity may be related to overall stiffness of the articulator or a specific movement direction of a particular articulator, or (more likely) some combination of the two, depending on the task requirements. While verification gestures were used in the current study to ensure that sampled muscles contributed to lower lip elevation and upper lip depression, the observed individual differences may be related to the above factors, as well as electrode placement, individual variations in subject muscular anatomy and movement variable differences (e.g., displacement, velocity), among others.

In summary, the present paradigm ensured that the presence of a task-dependent response observed during speech movement perturbation was a result of state-dependent modulation of afferent information, rather than the result of inadequate depolarization of motor neurons. Task-dependent speech motor organization apparently includes both feedforward control signals and afferent modulation. This interaction would act to minimize the degree of computation and precision required for the motor plan and allow the dynamics of the speaking process to assist in putting the final touches on speech motor output.

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References

Abbs JH, Gracco VL (1984) Control of complex motor gestures: orofacial muscle responses to load perturbations of the lip during speech. J Neurophysiol 51:705–723

Abbs JH, Gracco VL, Cole KJ (1984) Control of coordination: sensorimotor mechanisms in speech motor programming. J Motor Behav 16:195–232

Abbs JH, Shaiman S, Gracco VL, Cole KJ (1985) Task-dependent sensorimotor actions are inherent in speech motor programs. Soc Neurosci 11:76

Barlow SM, Cole KJ, Abbs JH (1983) A new head-mounted lip-jaw movement transduction system for the study of motor speech disorders. J Speech Hear Res 26:283–288

Bernstein N (1967) The coordination and regulation of movements. Pergamon Press, New York

Brooke JD, McIlroy WE, Staines WR, Angerilli PA, Peritore GF (1999) Cutaneous reflexes of the human leg during passive movement. J Physiol 518:619–628

Cole KJ, Gracco VL, Abbs JH (1984) Autogenic and nonautogenic sensorimotor actions in the control of multiarticulate hand movements. Exp Brain Res 56:582–585

Cordo PJ, Nashner LM (1982) Properties of postural adjustments associated with rapid arm movements. J Neurophysiol 47:287–302

Flanagan JR, Wing AM (1993) Modulation of grip force with load force during point-to-point movements. Exp Brain Res 95:131–143

Flanagan JR, Wing AM (1995) The stability of precision grip force during cyclic arm movements with a hand-held load. Exp Brain Res 105:455–464

Flanagan JR, Tresilian JR, Wing AM (1993) Coupling of grip force and load force during arm movements with grasped objects. Neurosci Lett 152:53–56

Folkins JW, Abbs JH (1975) Lip and jaw motor control during speech: responses to resistive loading of the jaw. J Speech Hear Res 18:207–220

Folkins JW, Linville RN (1983) The effects of varying lower-lip displacements upon upper lip movements: implications for the coordination of speech movements. J Speech Hear Res 26:209–217

Folkins JW, Zimmermann GN (1981) Jaw-muscle activity during speech with the mandible fixed. J Acoust Soc Am 69:1441–1445

Forssberg H, Grillner S, Rossignol S (1975) Phase dependent reflex reversal during walking in chronic spinal cats. Brain Res 85:103–107

Fowler CA, Rubin P, Remez RE, Turvey MT (1980) Implications for speech production of a general theory of action. In: Butterworth B (ed) Language production, vol 1. Speech and talk. Academic, London, pp 374–420

Gracco VL (1994) Some organizational characteristics of speech movement control. J Speech Hear Res 37:4–27

Gracco VL, Abbs JH (1985) Dynamic control of the perioral system during speech: kinematic analyses of autogenic and nonautogenic sensorimotor processes. J Neurophysiol 54:418–432

Gracco VL, Abbs JH (1989) Sensorimotor characteristics of speech motor sequences. Exp Brain Res 75:586–598

Hirose H, Kiritani S, Sawashima M (1982) Velocity of articulatory movements in normal and dysarthric subjects. Folia Phoniatr Logop 34:210–215

Kelso JAS, Tuller B, Harris KS (1983) A 'dynamic pattern' perspective on the control and coordination of movement. In: MacNeilage PF (ed) The production of speech. Springer, New York, pp 137–173

Kelso JAS, Tuller B, Vatikiotis-Bateson E, Fowler CA (1984) Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. J Exp Psychol Hum Percept Perform 10:812–832

Kennedy JG, Abbs JH (1979) Anatomic studies of the perioral motor system: foundations for studies in speech physiology. In: Lass N (ed) Speech and language: advances in basic research and practice, vol 1. Academic, New York, pp 211–270

Kirk RE (1982) Experimental design: procedures for the behavioral sciences, 2nd edn. Wadsworth Inc. Belmont, CA

Kollia BK, Gracco VL, Harris KS (1992) Functional organization of velar movements following jaw perturbation. J Acoust Soc Am 91:2474

Lewis GN, Byblow WD, Carson RG (2001) Phasic modulation of corticomotor excitability during passive movement of the upper limb: effects of movement frequency and muscle specificity. Brain Res 900:282–294

Marsden CD, Merton PA, Morton HB (1981) Human postural responses. Brain 104:513–534

Munhall KG, Löfqvist A, Kelso JAS (1994) Lip-larynx coordination in speech: effects of mechanical perturbations to the lower lip. J Acoust Soc Am 95:3605–3616

Nashner LM, Cordo PJ (1981) Relation of automatic postural responses and reaction-time voluntary movements of human leg muscles. Exp Brain Res 43:395–405

O'Dwyer NJ, Quinn PT, Guitar BE, Andrews G, Neilson PD (1981) Procedures for verification of electrode placement in emg studies of orofacial and mandibular muscles. J Speech Hear Res 24:273–287

Quintern J, Berger W, Dietz V (1985) Compensatory reactions to gait perturbations in man: short- and long-term effects of neuronal adaptation. Neurosci Lett 62:371–376
Shaiman S (1989) Kinematic and electromyographic responses to perturbation of the jaw. J Acoust Soc Am 86:78–88
Sussman HM, MacNeilage PF, Hanson RJ (1973) Labial and mandibular dynamics during the production of bilabial consonants: preliminary observations. J Speech Hear Res 16:397–420
Swinnen SP, Dounskaia N, Verschueren S, Serrien DJ, Daelman A (1995) Relative phase destabilization during interlimb coordination: the disruptive role of kinesthetic afferences induced by passive movement. Exp Brain Res 105:439–454
Traub MM, Rothwell JC, Marsden CD (1980) A grab reflex in the human hand. Brain 103:869–884