Special Education and Communication Disorders
Faculty Publications

Department of Special Education and
Communication Disorders

2007

Modulation Of The Trigeminofacial Pathway During Syllabic Speech

Meredith Estep
University of Kansas, mestep@ku.edu

Steven M. Barlow
University of Nebraska-Lincoln, steven.barlow@unl.edu

Follow this and additional works at: http://digitalcommons.unl.edu/specedfacpub

Part of the Special Education and Teaching Commons

MODULATION OF THE TRIGEMINOFACIAL PATHWAY DURING SYLLABIC SPEECH

Meredith Estep, B.A. and **Steven M. Barlow, Ph.D.**
Department of Speech-Language-Hearing Sciences and Programs in Neuroscience, Human Biology, and Bioengineering University of Kansas

Abstract

The human orofacial system is richly endowed with low threshold, slowly adapting mechanoreceptors that respond to self-generated movements and external loads. The functional linkage between these afferents and the recruitment of motor units in the lower face during the dynamics of speech is unknown. Mechanically evoked activity in the orbicularis oris muscles was studied in young human female adults (N=10) during a lip force recruitment task associated with the repetition of the nonsense speech utterance "ah-**w**ah." This speech task involved the recruitment of perioral motor units against an elastic load. A skin contactor probe coupled to a servo-controlled linear motor delivered punctate ipsilateral mechanical inputs (25 ms duration, 1800 μm displacement) to the glabrous surface of the upper lip in order to index the modulation and specificity of the compound trigeminofacial response as a function of speech force recruitment threshold (Ft). Modulation of the early (Ft = 0.2N) and later (Ft = 1.0N) components of the evoked perioral response was found at the two force thresholds. Beginning at approximately 60 ms post-stimulus, a significant suppression response was found among lower lip EMG recording sites and its magnitude was greatest when the mechanical perturbation occurred during the early phase of lip force recruitment. Variation in the lip force trajectories was manifest by a greater difference in net interangle force associated with lip perturbations indexed to the early Ft. This was interpreted to reflect the operation of a feedforward mechanism which may play a more significant role during an evolving speech action. Thus, the application of servo-controlled mechanosensory inputs effectively indexed the excitability of the facial motor nucleus during production of a simple speech phrase. Future studies are needed to explore mechanisms of short-term adaptation and trigeminofacial modulation during propositional speech in health and disease.

Keywords

Compound Perioral Response; Orbicularis Oris; Active Force; Mechanical Stimulation; Electromyography

1. Introduction

Direct human microneurographic recordings from orofacial afferents have confirmed that sensory flow conducted along trigeminal pathways is abundant and apparently related to movement, force, and tissue contacts associated with speech, mastication, mime, as well as external perturbations delivered to the perioral tissues (Johansson et al., 1988; Nordin and

Correspondence: M. Estep, B.A., 1000 Sunnyside Avenue, SPLH Dole 3001, University of Kansas, Lawrence KS 66045-7555, mestep@ku.edu, TL (785) 864-4447, FX (785) 864-4403.

Thomander, 1989). The coupling between sensory and motor fields in the perioral system can be seen following tactile stimulation of circumoral tissues which causes reflex contraction of specific muscles, usually those underlying the area of stimulation. This fixed relation between the locus of the stimulus and the particular muscles that contract is called *local sign* (Gordon, 1991). The early excitatory component of the evoked perioral response, known as R1 or E1, manifests local sign with the EMG response predominantly ipsilateral and proximal to the stimulus (Larson et al., 1978; Barlow, 1991, Barlow and Bradford, 1996; McClean and Smith, 1982; Smith et al., 1987; Wohlert, 1996) when using a mechanical tap, stretch, or tangential cutaneous stimulation applied to the perioral region. A less consistent latter excitatory component, known as R2 (*or* E2), with an onset latency of approximately 30–45 ms is complex in structure and tends to adapt rapidly to repeated stimulation. Neural pathways mediating R1 are presumed to be brainstem in origin. Pathways involved in mediating R2 are not well understood, but are speculated to involve suprabulbar pathways based primarily on latency analysis and lesion studies (Barlow and Bradford, 1992; Larson, 1977).

Driving the perioral response using punctate mechanical stimuli in the presence of subject-generated steady-state lip muscle activation effectively potentiates the early component of the trigeminofacial reflex. The R1 component of the mechanically evoked perioral response shows monotonic growth in amplitude with successive increases in the level of sustained isometric force without consistent activation of R2 (Barlow, 1991; Barlow and Bradford, 1996). The spatiotemporal organization of the evoked perioral response takes on added complexity with additional components under the more demanding task dynamics (i.e., movements specific to an experimental task) required during a ramp-and-hold task (Andreatta et al., 1994, 1996).

Small movements and forces are strongly dependent on peripheral inputs perhaps in part due to cutaneous and muscle receptors exhibiting their greatest sensitivity to small amplitude input signals (Goodwin et al., 1975; Knibestol, 1975; Knibestol and Vallbo, 1970; Matthews and Stein, 1969; Poppele and Bowman, 1970). The production of speech is dominated by small forces and fine adjustments in position (Barlow and Muller, 1991; Barlow and Rath, 1985; Muller et al., 1985). The objective for the current experimental report was to index evoked perioral response modulation and specificity as a function of recruitment force (early versus mid-gesture) during production of a simple di-syllablic speech phrase using a punctate mechanical input delivered under position-feedback. Well-defined early perioral responses followed the expected pattern of trigeminofacial response specificity or local sign. However, a large amplitude, long latency suppression (S1) component in the non-stimulated lip was significantly dependent on the force recruitment threshold (Ft) during lip rounding. This was interpreted to reflect a feedforward process manifest in the electromyograms of the non-perturbed lip. Thus, the punctate mechanical stimulation presented to the upper lip in normal young adult females at early (Ft = 0.2N) and mid-contraction (Ft = 1.0N) phases of lip force recruitment, yielded a differential expression of perioral responsiveness during speech syllable production.

2. Results

The spatiotemporal organization of the mechanically evoked perioral response was highly dependent upon the phase of force recruitment associated with production of "ah-**w**ah." This response included two excitatory components (R1 ~ 15–30 ms and R2 ~ 30–50 ms) and a suppression component (S1 ~ 60–120 ms). The R1 and R2 components were consistently observed at the ipsilateral homonymous muscle stimulation site (OOS-Right), and the R2/S1 response complex was observed in upper and lower lip contralateral to the mechanical input (Figures 1 and 2). Task dynamics and the phase of force recruitment (early vs. mid-contraction triggering of the stimulus) are determinants in the specificity of mechanosensory modulation of perioral motor output during speech production.

Force threshold (Ft) was a significant within-subjects main effect for potentiation of the compound perioral response [$F(1,108) = 4.62$, $p < 0.05$]. The response to mechanical stimuli presented at the early force threshold (Ft = 0.2N, mean = −3446.7 μV-sec, se = 82.2) was 49% larger than the overall response to stimuli presented at the mid-contraction force threshold (Ft = 1.0N, mean = −1689.4 μV-sec, se = 53.8). The composite response observed in the OOI-R had the largest difference between the two thresholds, and the OOS-L showed the smallest difference in composite response between the two thresholds. OOS-L was the only muscle to show higher mean partial sum of the composite reflex at the mid-contraction versus early Ft (Table 1). A significant two-way between-within interaction was found between Ft and the latency analysis window [$F(2,108) = 4.33$, $p < 0.05$]. The partial sum integral of the reflex significantly differed depending on the phase of muscle force recruitment and the specific reflex component being observed. A 41.6% increase in suppression was observed when the stimuli occurred during the early phase of the dynamic motor task (Table 2), but only about 5% difference was observed between the two thresholds for the first and second windows, corresponding to R1 and R2 respectively. The post-hoc paired-samples t-tests showed that the two means observed between early and mid-contraction thresholds are significantly different only in the suppression component [$t(39) = −2.26$, $p < .05$]. Therefore, the significant interaction effect is presumably due to the significantly different means observed at the early vs. mid-contraction Ft during the suppression phase of the trigeminofacial response.

The stability of the interangle lip force trajectory associated with production of the disyllabic speech utterance "ah-**w**ah" was remarkably stable for the two control (NO STIM) and two stimulation (STIM) conditions. The pooled mean lip force trajectories and 95% confidence intervals for each of the four conditions are shown graphically in Figure 3. Peak force for each of the 4 conditions was well within the 1.5N to 2.0N criterion force range with little variability. Evidence of reflex effects can be seen in the interangle lip force records by subtracting the control force trajectory (NO STIM) from the force trajectory obtained during the lip stimulation condition (STIM). As shown in Figure 4, the net force due to reflex effects appears to be considerably greater for the Ft = 0.2N condition which is consistent with the pattern of greater overall reflex modulation observed in the IEMG records.

3. Discussion

Modulation and specificity of the S1 component of the evoked perioral response has been demonstrated in the current study to be dependent upon the phase of lip force recruitment (early versus mid-contraction) associated with the production of the speech gesture "ah-**w**ah." The homonymous muscle (OOS-R) and lower lip muscle (OOI-R and OOI-L) recording sites yielded the greatest response magnitudes when the mechanical perturbations occurred during the early phase (Ft = 0.2N) of lip force recruitment. The presence of significant EMG modulation during the early recruitment phase among the non-stimulated muscle sites, particularly the lower lip, suggests that the operation of a feedforward mechanism may play a more significant role during an evolving speech action. Consistent with the modulation in perioral EMG, a concomitant change in net interangle lip force was also found suggesting a form of load compensation to the relatively brief, 25 millisecond upper lip perturbations used in the present study. This form of sensorimotor reorganization is consistent with the responses observed in nonperturbed lip during speech production by Shaiman and Gracco (2002). As shown in Figure 5, a significant suppression component occurring between 60 and 120 ms was manifest among orbicularis oris recording sites, especially when the indexing mechanical stimulus was presented during the early phase (Ft = 0.2N) of lip force recruitment. The same mechanical stimulus indexed at mid-contraction during lip rounding for "ah-**w**ah" was significantly less effective in modulating the perioral response, suggesting the terminal phase of lip force recruitment represents a transition to an open loop control mechanism and thus less amenable to feedback modification in the presence of external perturbations.

The literature supports the notion that increasing task dynamics by requiring subjects to modulate force or movement results in a compound trigeminofacial sensorimotor response which is dependent on the rate and phase of muscle force recruitment. This has been demonstrated during non-speech oromotor force behaviors (Andreatta et al., 1994, 1996; Barlow, 1991, 1998) as well as preparatory movements for speech (McClean, 1991; McClean and Clay, 1994). Alternatively, during static non-speech conditions such as rest and steady state isometric force maneuvers, the R2 late component of the mechanically evoked perioral response is typically elusive in normal subjects. However, in the current study, the presence of a suppression component (S1) dependent on lip rounding force was complemented by the presence of a remarkably consistent R2 component. The S1 component showed a parsum amplitude modulation of approximately 41.6% whereas the shorter latency R2 component only manifested 4.6% change between the early and mid-contraction indexed perturbations. The principal suprabulbar relays and pathways, including trigeminal lemniscus, ventroposteromedial nucleus of thalamus, and orofacial sensorimotor cortices, are presumed to mediate R2 and S1. What is the functional significance of the R2 component when mechanical perturbations are delivered during the dynamics of speech? An experimental approach involving functional neuroimaging and electrophysiological monitoring in a perturbation paradigm could provide insight to this question.

The encoding of force by the brain is central to models of movement, and relevant to speech motor control. The relation between limb force control and neural firing patterns in primate motor cortex is strongly correlated with the rate and direction of force change (Evarts, 1968; Georgopolous et al., 1992; Hepp-Reymond et al., 1978, 1999; Humphrey et al., 1970; Moran and Schwartz, 1999; Smith et al., 1975) and preferred-torque directions biased toward limb-flexor and limb-extensor torques (Herter et al., 2007; Kurtzer et al., 2006). Recent evidence suggests that the primary motor cortex plays a role in setting sensorimotor memory for fingertip forces during grip force (Berner et al., 2007). Primary motor cortex has also been shown to encode functional muscle synergies (Holdefer and Miller, 2002). The cortical mechanisms involved in the regulation of muscle dynamics during the early phases of force recruitment (Cheney and Fetz, 1980; Evarts et al., 1983; Fromm and Evarts, 1977; Sanes and Evarts, 1983) may be especially important for orofacial muscles that are characterized by small motor units which produce finely graded forces for speech (Barlow and Bradford, 1992; Barlow et al., 1999). The complex articulatory dynamics evident among facial muscles during speech is similar in many ways to the precise movements and forces generated by hand and fingers. During speech production, the muscles of the perioral system exhibit a streaming repertoire of phasic adjustments in force from resting tonic activation to approximately 10% of the maximum voluntary contraction level (Barlow and Muller, 1991; Muller et al., 1985). The response properties of motor cortex are well suited to support the functional synergies which are presumed to play a significant role in the control of phasic lip movements for speech. Consistent with this view is the finding from a recent study which suggests that primary motor cortex may participate in the modulation of the reflexive compensatory motor responses in lip muscles during speech (Ito et al., 2005).

Consistent with observations in primate motor cortex (Cheney and Fetz, 1980; Fromm and Evarts, 1977), our findings suggest that the orofacial system may utilize mechanosensory information differentially for the early versus later phases of lip force output. During speech articulation, longer latency reflex actions presumably involving primary motor cortex correct for the effects of external movement disturbances (Ito et al., 2005). Mechanical inputs delivered to a dynamically contracting lip muscle produce a compound evoked perioral response characterized by phases of excitation and suppression (Andreatta et al., 1994) that are not observed during static force conditions (Barlow, 1991). Compensatory lip movements demonstrate a well-calibrated readjustment (Gracco and Abbs, 1985). Similar reports of rapid modifications of aimed arm movements to changes in target location further emphasize the

ability to modify movements throughout the motor act (Georgopoulos et al., 1983; Soechting and Lacquaniti, 1983).

The complex nature of perioral sensorimotor reactions to punctate cutaneous stimuli in young adults has been demonstrated as a function of force recruitment level in the present report. The mechanically evoked perioral response is an important indexing probe of facial motoneuron excitability that may be used to gain insight on the development and maintenance of related neural circuits involved in the emergence of certain motor skills such as speech (Barlow, 1998). Given the dynamics inherent to speech motor control, it is possible to envision how gating or modulation of cutaneous input might produce more significant influences on lower motoneurons during certain phases of movement in the selection, sequencing, and activation of muscle subgroups in the orofacial system. Future studies are needed to explore mechanisms of short-term adaptation and trigeminofacial modulation during a more complex form of propositional speech in health and disease.

4. Experimental Procedure

Participants

Given the gender differences in perioral tissue biomechanics during voluntary force (Barlow and Muller, 1991; Barlow and Rath, 1985), only native English speaking female subjects (N=10, mean age 22 years) were used for this experiment. Written informed consent was obtained from each participant in accordance with the guidelines set forth by the University of Kansas Human Subjects Committee. Participants were seated in a dental chair with occipital support provided to stabilize the head. The experimental method consisted of three components: electromyography, lip force control, and mechanical stimulation.

EMG Recording and Jaw Stabilization

The spatial distribution of mechanically evoked EMG activity was mapped bilaterally for all subjects at four skin sites overlying the orbicularis oris superior (OOS) and orbicularis oris inferior (OOI) using custom-designed low profile 4 mm diameter Ag/AgCl hydrogel surface electrodes placed on the nonglabrous skin over the target muscle areas (OOS-Left, OOS-Right, OOI-Left, OOI-Right) with 5 mm of separation and within 1 mm of the upper or lower lip vermilion border. Biopotentials from each electrode pair were conditioned by a Grass P511 bioamplifier (gain = 20K, BP 0.1 – 3 KHz, $Z \leq 5k\Omega$). A bite block was made for each subject to effectively stabilize the jaw during the speech task. It was placed between the upper and lower molars on the left side of the subject's mouth. After electrode placement, subjects were required to perform movements of the lips independent of the jaw to assess if the myogenic and kinematic outputs were appropriate for the muscle recording site (Blair and Smith, 1986).

Force Recording

Interangle force was sampled from the corners of the mouth using a specially designed stainless steel cantilever instrumented with strain gages. The spring constant for this transducer was 0.22 N/mm. Passive elastic recoil of the lips was sufficient to maintain the proper orientation of the device relative to the chin. The analog lip force signal was conditioned by a bridge amplifier (DC-coupled) and low-pass filtered (−3 dB @ 50 Hz, 3-pole Butterworth), and displayed to the participant in real-time on a digital oscilloscope. A peak force 'target' window was represented on the oscilloscope using a pair of horizontal cursors set at the 1.5N and 2.0N force levels. Visual feedback of lip force permitted subjects to produce consistent peak force levels that fell within this target window. The subject-generated force recruitment trajectory associated with production of the speech utterance "ah-**w**ah" was monophasic and consisted

of lip rounding and medialization of the oral angles followed by release for the final vowel / a/.

Mechanical Stimulation

A custom designed linear servo motor operating under position feedback was used to deliver unilateral mechanical stimulation to the glabrous upper-right lip. A 16-bit deglitched digital-to-analog converter was programmed to drive the linear motor to produce monophasic inward displacements of the lip vermilion of approximately 1800 μm using a 25 ms duration pulse. These punctate stimuli were triggered to discrete early (Ft = 0.2N) and mid-contraction (Ft = 1.0N) force threshold points associated with lip rounding during production of the speech phrase "ah-**w**ah" (Figure 6). The servo was triggered synchronously to absolute target force threshold crossings (i.e., the *rate* of force recruitment was not used to trigger the servo). A 6-point (2×3 array) skin contactor was used as the cutaneous probe interface (Barlow, 1991).

Design

A complete experiment consisted of: upper lip perturbations presented at 2 speech force recruitment threshold conditions (STIM), and matching control conditions (NO STIM) in which no stimulation was given. The blocking order (*i.e.*, Ft = 0.2N STIM, Ft = 1.0N STIM, Ft = 0.2N NO STIM, and Ft = 1.0N NO STIM) was counterbalanced among subjects. Upon completion of each test block, subjects were given a 3-minute rest period and permitted to rehydrate while the experimenter checked the electrodes and initialized a new data file. Thus all subjects were required to produce a total of 240 repetitions (60 trials/block) of the speech utterance "ah-**w**ah" with lip rounding force trajectories that were within the criterion of 1.5N to 2.0N peak compression force. A microprocessor was used to replay a digitized model of the target word "ah-**w**ah" (utterance duration = 792 ms) to each subject for rate, loudness, and stress control. Test subjects produced this utterance approximately once every 5.5 sec until 60 acceptable trials were completed for a block.

Data Analysis

All signals (trigger pulse-stimulus pulse, probe displacement, probe force, active lip force, and the four perioral EMG channels) were digitized in real time at 10 KHz on 16-bits of vertical resolution into fixed buffers of 500 ms which included a 200 ms pre-trigger sampling buffer. The EMG channels were demeaned, full-wave rectified, and integrated (2.5 ms time constant) prior to signal averaging the 60 trials for each of the four block conditions using a special signal processing routine written in MATLAB. The averaged data were subjected to waveform discrimination, and segregated as a function of lip force threshold for the speech task. The integrated electromyographic (IEMG) envelope associated with lip force recruitment during the NO STIM conditions were digitally subtracted from the STIM conditions with trigger points aligned at the two force thresholds in order to yield a NET mechanically evoked perioral response for each force recruitment condition.

The NET IEMG waveforms were then subjected to a partial sums integral (PARSUMS, Minitab v.14) beginning at stimulus point T_0 through the first 120 ms of the post-trigger window. Three analysis windows were selected to reflect early (first window) versus late (second and third windows) components of neural processing in the present data set, presumably reflecting bulbar versus suprabulbar influences on the evoked IEMG perioral response. The window boundaries assigned to the IEMG waveform arrays were as follows: 18.0–39.9 ms associated with the growth of the R1 component, 40–59.9 ms to distinguish the R2 component, and 60.0–120.0 ms to encompass the S1 component. The PARSUMS analysis method was utilized because of its sensitivity to cumulative electrophysiological activity as a function of time among the perioral muscle recording sites, thereby eliminating the dependence to search for discrete peaks and valleys in the complex evoked response profile during an active motor pattern.

The SPSS statistical software program was used to perform repeated measures ANOVA to evaluate significant factors that affect the dependent variable of partial sums. Within-subjects factor was the partial sum measure obtained at each force threshold (Ft = 2 levels: 0.2N or 1.0N). Between-subjects factors were orbicularis oris muscles (muscle = 4 levels: OOS-R, OOS-L, OOI-R, OOI-L) and analysis domain (window = 3 levels: 18–39, 40–59, 60–120 ms).

References

Andreatta RD, Barlow SM, Finan DS. Modulation of the mechanically evoked perioral reflex during active force dynamics in young adults. Brain Res 1994;646:175–179. [PubMed: 8055337]

Andreatta RD, Barlow SM, Finan DS, Biswas A. Mechanosensory modulation of perioral neuronal groups during active force dynamics. J Speech Hear Res 1996;39:1006–1017. [PubMed: 8898254]

Barlow SM, Rath EM. Maximum voluntary contraction levels in the upper and lower lip of humans. J Speech Hear Res 1985;28:373–376. [PubMed: 4046578]

Barlow SM. Modulation of mechanically evoked perioral reflexes during active force. Brain Res 1991;565:330–336. [PubMed: 1842699]

Barlow SM, Muller EM. The relation between interangle span and in vivo resultant force in the perioral musculature. J Speech Hear Res 1991;34:252–259. [PubMed: 2046349]

Barlow SM, Bradford PT. Measurement and implications of orofacial muscle performance in speech disorders. J Hum Muscle Performance 1992;1:1–31.

Barlow SM, Bradford PT. Comparison of perioral reflex modulation in the upper and lower lip. J Spech Hear Res 1996;39:55–75.

Barlow SM. Real time modulation of speech-orofacial motor performance by means of motion sense. J Com Disord 1998;31:511–534.

Barlow, SM.; Bradford, PT.; Andreatta, RD. Handbook of Clinical Speech Physiology. Singular Publishing Group, Inc; San Diego, CA: 1999. Orofacial force physiology; p. 303-346.

Berner J, Schonfeldt-Lecuona C, Nowak DA. Sensorimotor memory for fingertip forces during object lifting: the role of the primary motor cortex. Neuropsychologia. 2007 Jan 18;Epub ahead of print

Blair C, Smith A. EMG recording in human lip muscles: can single muscles be isolated? J Speech Hear Res 1986;29:256–266. [PubMed: 3724118]

Cheney PD, Fetz EE. Functional classes of primate corticomotoneuronal cells and their relation to active force. J Neurophysiol 1980;44:773–791. [PubMed: 6253605]

Evarts EV. Relation of pyramidal tract activity to force exerted during voluntary movement. J Neurophysiol 1968;31:14–27. [PubMed: 4966614]

Evarts EV, Fromm C, Kroller J, Jennings VA. Motor cortex control of finely graded forces. J Neurophysiol 1983;49:1199–1215. [PubMed: 6864246]

Fromm C, Evarts EV. Relation of motor cortex neurons to precisely controlled and ballistic movements. Neurosci Lett 1977;5:259–265.

Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT. Interruption of motor cortical discharge subserving aimed arm movements. Exp Brain Res 1983;49:327–340. [PubMed: 6641831]

Georgopoulos AP, Ashe J, Smyrnis N, Taira M. The motor cortex and the coding of force. Science 1992;256:1692–1695. [PubMed: 1609282]

Goodwin GM, Hulliger M, Matthews BC. The effects of fusimotor stimulation during small amplitude stretching on the frequency-response of the primary ending of the mammalian muscle spindle. J Physiol (London) 1975;253:175–206. [PubMed: 128457]

Gordon, J. Spinal mechanisms of motor coordination. In: Kandel, ER.; Schwartz, JH.; Jessell, TM., editors. Principles of Neural Science. Elsevier; NY: 1991. p. 581-595.

Gracco VL, Abbs JH. Dynamic control of the perioral system during speech: kinematic analyses of autogenic and nonautogenic sensorimotor processes. J Neurophysiol 1985;54:418–432. [PubMed: 4031995]

Hepp-Reymond MC, Wyss UR, Anner R. Neuronal coding of static force in the primate motor cortex. J Physiol (Paris) 1978;74:287–291. [PubMed: 102775]

Hepp-Reymond MC, Kirkpatrick-Tanner M, Gabernet L, Qi HX, Weber B. Context-dependent force coding in motor and premotor cortical areas. Exp Brain Res 1999;128:123–133. [PubMed: 10473750]

Herter TM, Kurtzer I, Cabel DW, Haunts KA, Scott SH. Characterization of torque-related activity in primary motor cortex during a multi-joint postural task. J Neurophysiol. 2007in press

Holdefer RN, Miller LE. Primary motor cortical neurons encode functional muscle synergies. Exp Brain Res 2002;146:233–243. [PubMed: 12195525]

Humphrey DR, Schmidt EM, Thompson WD. Predicting measures of motor performance from multiple cortical spike trains. Science 1970;179:758–762. [PubMed: 4991377]

Ito T, Kimura T, Gomi H. The motor cortex is involved in reflexive compensatory adjustment of speech articulation. NeuroReport 2005;16:1791–1794. [PubMed: 16237328]

Johansson RS, Trulsson M, Olsson KA, Abbs JH. Mechanoreceptive afferent activity in the infraorbital nerve in man during speech and chewing movements. Exp Brain Res 1988;72:209–214. [PubMed: 3169190]

Knibestol M, Vallbo AB. Single unit analysis of mechanoreceptor activity from the human glabrous skin. Acta Physiol Scand 1970;79:178–195. [PubMed: 5475340]

Knibestol M. Stimulus-response functions of slowly adapting mechanoreceptors in the human glabrous skin area. J Physiol (London) 1975;245:63–80. [PubMed: 1127614]

Kurtzer I, Herter TM, Scott SH. Non-uniform distribution of reach-related and torque-related activity in upper arm muscles and neurons of primary motor cortex. J Neurophysiol 2006;96:3220–3230. [PubMed: 17005623]

Larson, CR. Lesion effects on the perioral reflex in awake monkeys. Paper presented to the American Speech and Hearing Association; Chicago. 1977.

Larson CR, Folkins JW, McClean MD, Muller EM. Sensitivity of the human perioral reflex to parameters of mechanical stretch. Brain Res 1978;146:159–164. [PubMed: 148310]

Matthews PB, Stein RB. The sensitivity of muscle spindle afferents to small sinusoidal changes of length. J Physiol (London) 1969;202:59–82. [PubMed: 4238988]

McClean MD, Smith A. The reflex responses of single motor units in human lower lip muscles to mechanical stimulation. Brain Res 1982;251:65–75. [PubMed: 7172010]

McClean MD. Lip muscle reflex and intentional response levels in a simple speech task. Exp Brain Res 1991;87:662–670. [PubMed: 1783035]

McClean MD, Clay JL. Evidence for suppression of lip muscle reflexes prior to speech. Exp Brain Res 1994;97:541–544. [PubMed: 8187864]

Moran DW, Schwartz AB. Motor cortical representation of speed and direction during reaching. J Neurophysiol 1999;82:2676–2692. [PubMed: 10561437]

Muller, EM.; Milenkovic, PH.; MacLeod, GE. Perioral tissue mechanics during ppeech production. In: DeLisi, C.; Eisenfeld, J., editors. Proceedings of the Second IMAC International Symposium on Biomedical Systems Modeling. North-Holland Publishers; Amsterdam, Netherlands: 1985. p. 363-371.

Nordin M, Thomander L. Intrafascicular multi-unit recordings from the human infra-orbital nerve. Acta Physiologica Scandinavica 1989;135:139–148. [PubMed: 2922998]

Poppele R, Bowman RJ. Quantitative description of linear behavior of mammalian muscle spindles. J Neurophysiol 1970;33:59–72. [PubMed: 4243791]

Sanes, J.; Evarts, EV. Regulatory role of proprioceptive input in motor control of phasic or maintained voluntary contractions in man. In: Desmedt, J., editor. Motor Control Mechanisms in Health and Disease. Raven Press; NY: 1983. p. 47-59.

Shaiman S, Gracco VL. Task-specific sensorimotor interactions in speech production. Exp Brain Res 2002;146:411–418. [PubMed: 12355269]

Soechting JF, Lacquaniti F. Modifications of trajectory of a pointing movement in response to a change in target location. J Neurophysiol 1983;49:548–564. [PubMed: 6834087]

Smith AM, Hepp-Reymond MC, Wyss UR. Relation of activity in precentral cortical neurons to force and rate of force change during isometric contractions of finger muscles. Exp Brain Res 1975;23:315–332. [PubMed: 810360]

Smith A, McFarland DH, Weber CM, Moore CA. Spatial organization of human perioral reflexes. Exp Neurol 1987;98:233–248. [PubMed: 3666076]

Wohlert AB. Reflex responses of lip muscles in young and older women. J Speech Hear Res 1996;39:578–589. [PubMed: 8783136]
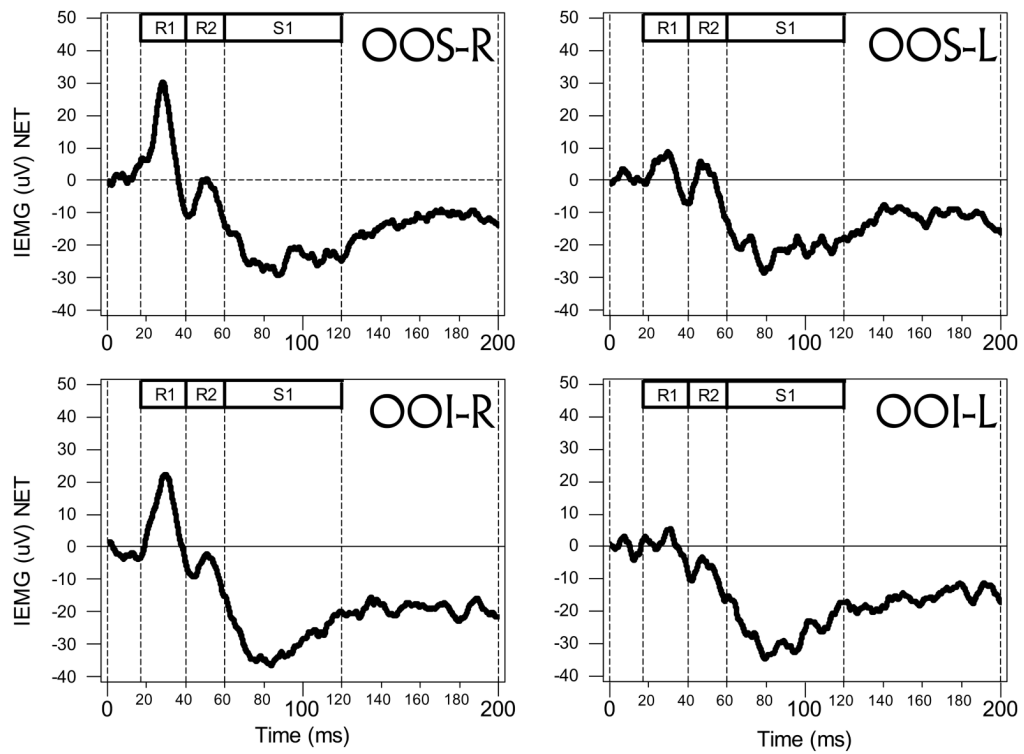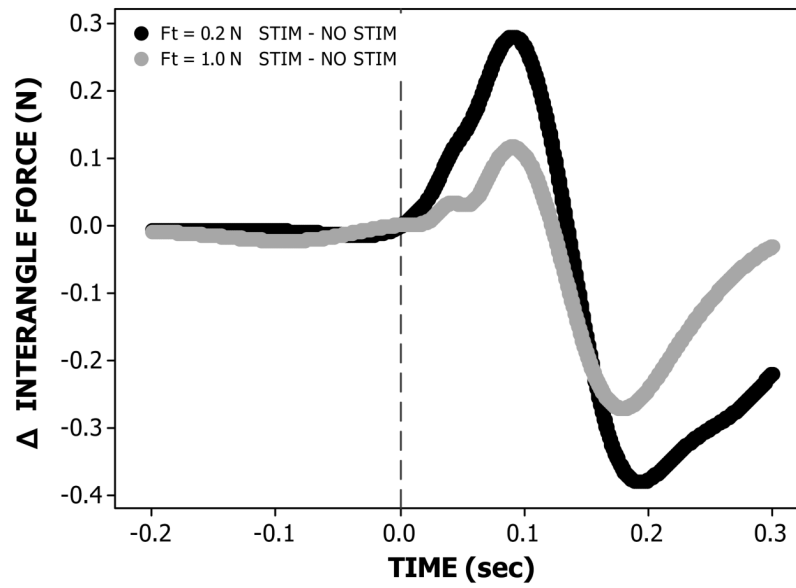
Figure 1.
R1/R2/S1 Trigeminofacial modulation NET response, Ft = 0.2N. Perioral reflex recorded in each quadrant of the orbicularis oris muscle. Each composite indicates the response to mechanical stimuli presented at the early force threshold across all subjects.
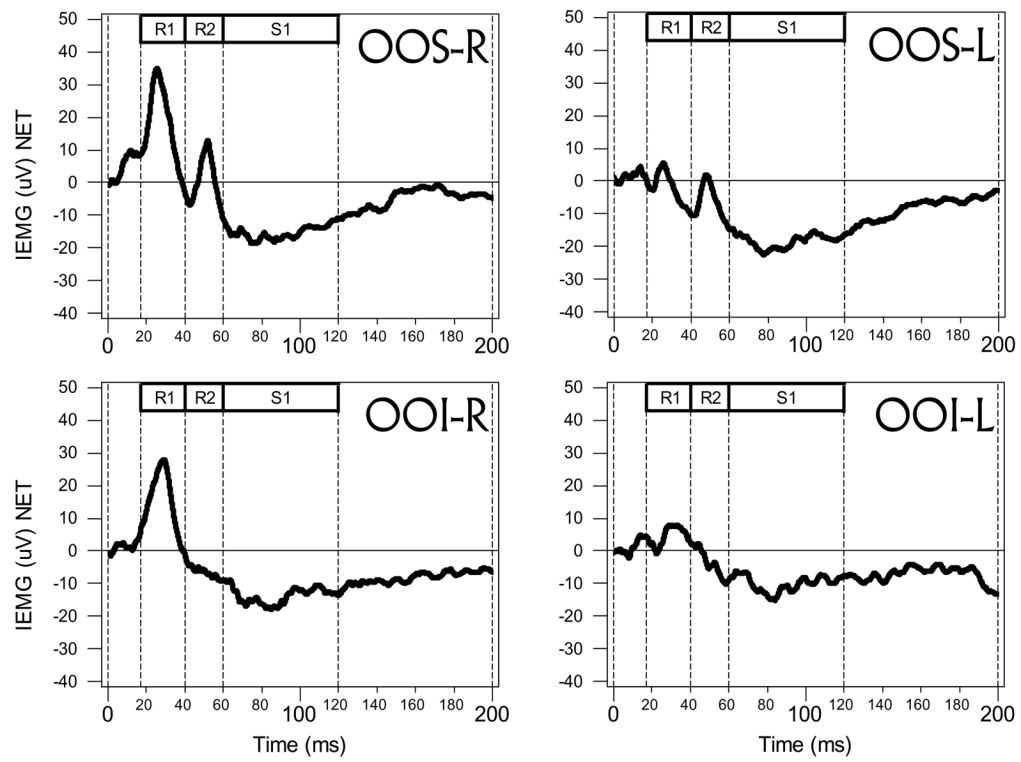
Figure 2.
R1/R2/S1 Trigeminofacial modulation NET response, Ft = 1.0N. Perioral reflex recorded in each quadrant of the orbicularis oris muscle. Each composite indicates the response to mechanical stimuli presented at the mid-contraction force threshold across all subjects.
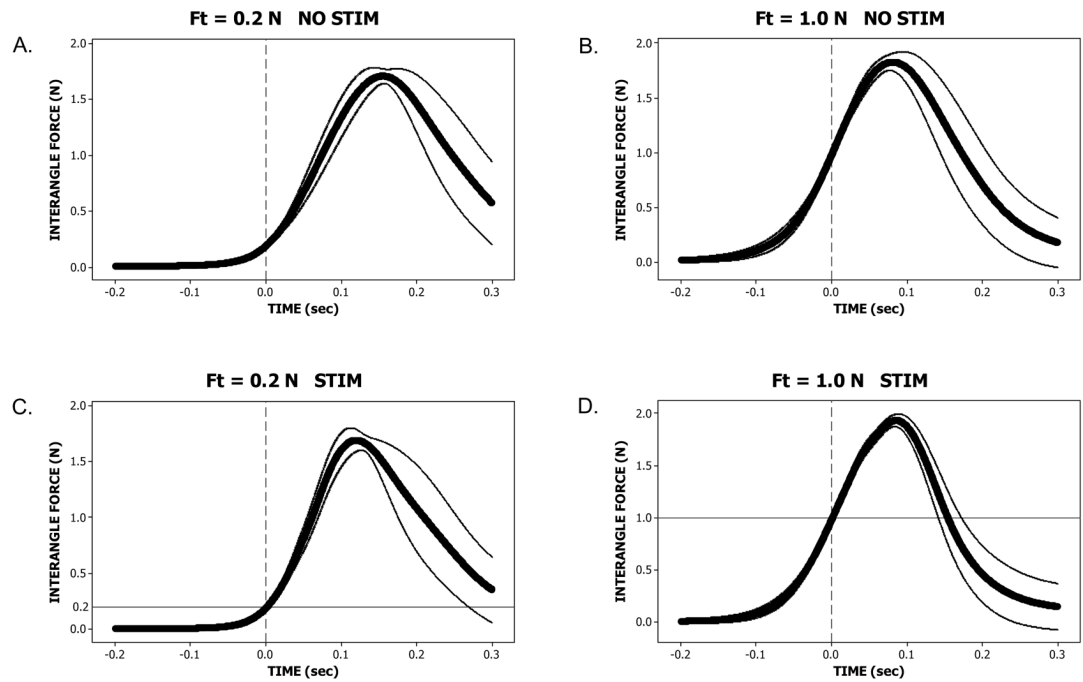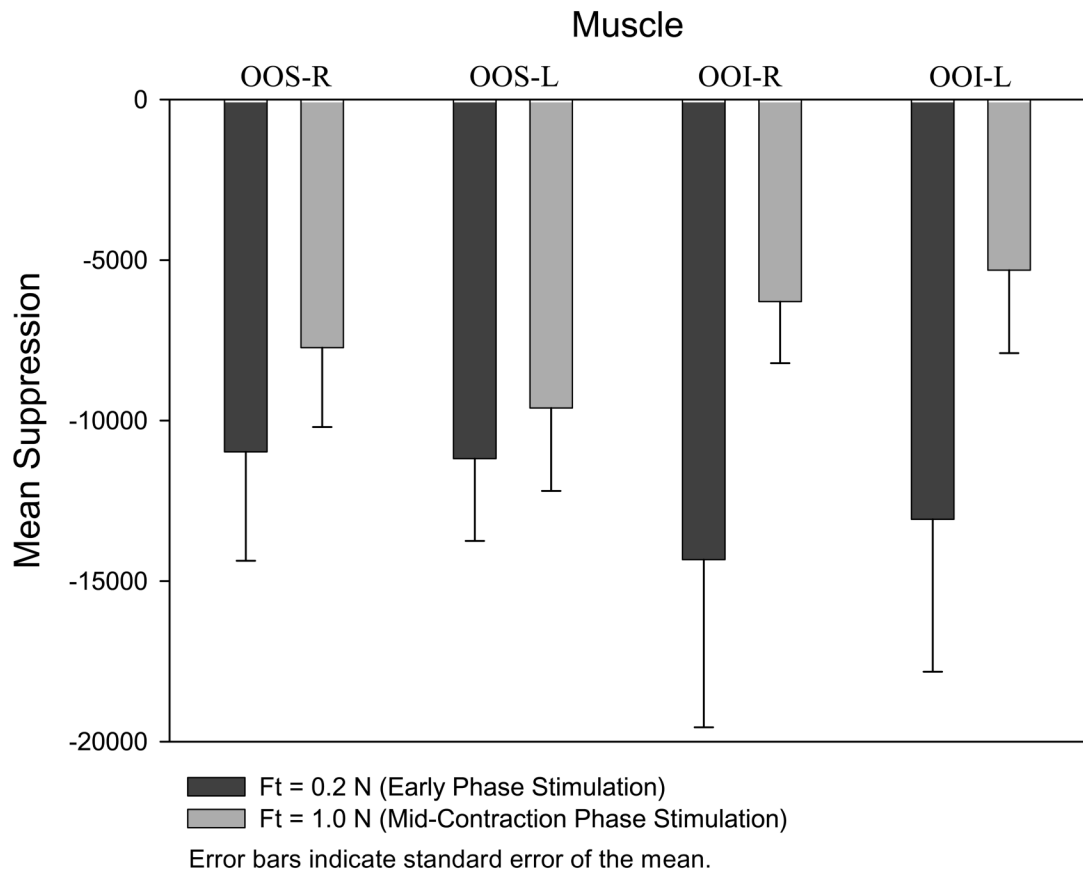
Figure 3.
The pooled mean lip force trajectories for all 10 test subjects and associated 95 percent confidence intervals for each of the four conditions are shown graphically. Reference lines indicate trigger points for mechanical stimulation (STIM Conditions) and force threshold levels used for real-time waveform discrimination.

PERTURBATION MINUS CONTROL LIP FORCE

Figure 4.
Net interangle lip force derived by subtracting pooled interangle force (NO STIM – control condition) from the pooled interangle force (STIM – experiment condition).

Figure 5.
Suppression responses associated with early versus mid-contraction phase stimuli. Comparison of the suppression component observed in each muscle.
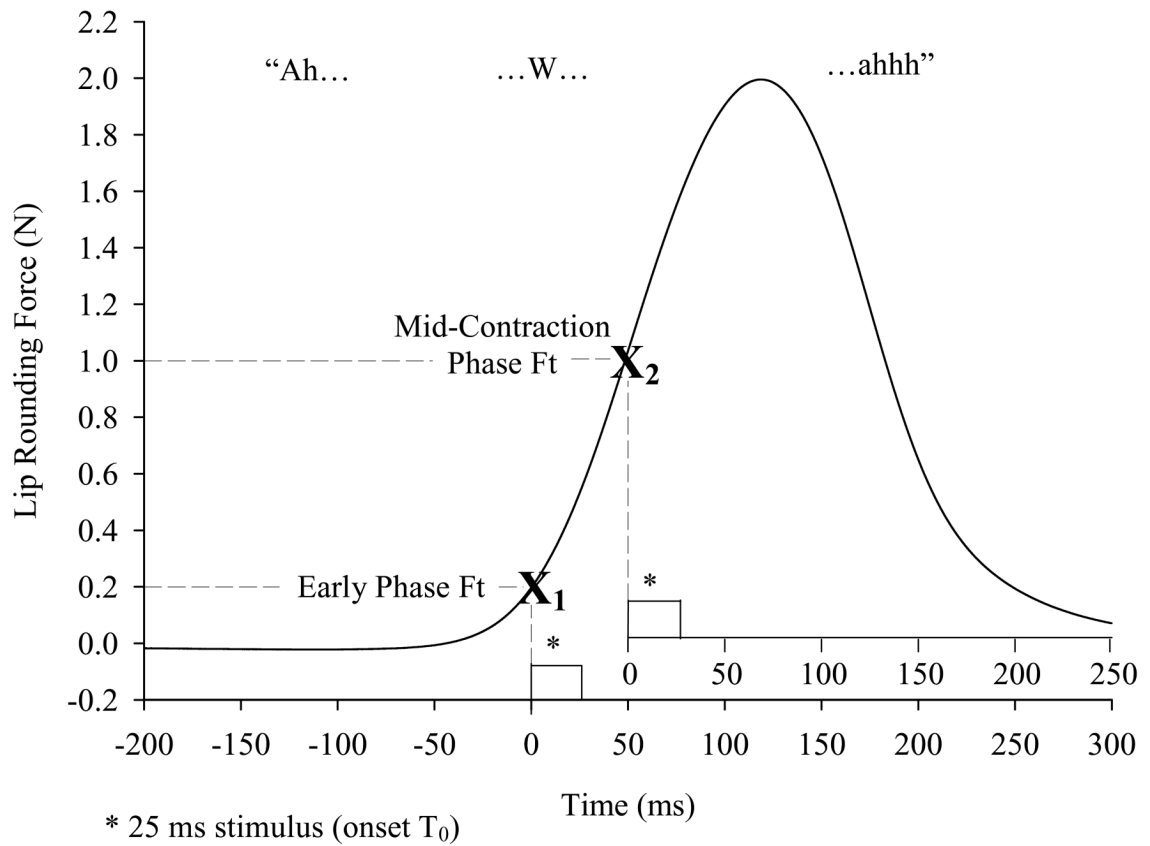
Figure 6.
Lip force recruitment thresholds. Interangle lip force task representative of the two experimental conditions. The punctate mechanical stimulus was triggered using real-time waveform-threshold discrimination when the early (Ft = 0.2N) or mid-contraction (Ft = 1.0N) threshold event was met.

Table 1

Mean partial sum (μV-sec, standard error in brackets) for each muscle at different force thresholds

Muscle	Early Ft: 0.2 N	Mid-Contraction Ft: 1.0 N	Δ re: Early Ft
OOS-R	−2423.4 (1637.9)	−856.4 (1347.9)	−64.7%
OOS-L	−3325.4 (1348.2)	−3460.8 (1199.0)	+4.1%
OOI-R	−3771.7 (2221.0)	−936.9 (1058.5)	−75.2%
OOI-L	−4266.5 (1955.3)	−1503.3 (1085.2)	−64.8%
TOTAL	−3446.7 (900.8)	−1689.4 (589.6)	−51.0%

Table 2

Mean partial sum (μV-sec, standard error in brackets) for each window at different force thresholds

Window	Early Ft: 0.2 N	Mid-Contraction Ft: 1.0 N	Δ re: Early Ft
R1	2348.4 (381.5)	2477.5 (551.8)	+5.2%
R2	−294.8 (386.6)	−308.9 (435.8)	−4.6%
S1	−12393.8 (1991.3)	−7236.7 (1185.0)	−41.6%