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HIGHLIGHTED TOPIC | *Neural Control of Movement*

Fast force-generation dynamics of human articulatory muscles

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Ito, Takayuki, Emi Z. Murano, and Hiroaki Gomi. Fast force-generation dynamics of human articulatory muscles. *J Appl Physiol* 96: 2318–2324, 2004. First published February 27, 2004; 10.1152/japplphysiol.01048.2003.—To explore the mechanisms of speech articulation, which is one of the most sophisticated human motor skills controlled by the central nervous system, we investigated the force-generation dynamics of the human speech articulator muscles [orbicularis oris superior (OOS) and inferior (OOI) muscles of the lips]. Short-pulse electrical stimulation (300 μs) with approximately three or four times the sensation threshold intensity of each subject induced the muscle response. The responses of these muscles were modeled as second-order dynamics with a time delay (TD), and the model parameters [natural frequency (NF), damping ratio (DR), and TD] were identified with a nonlinear least mean squares method. The OOS (NF: 6.1 Hz, DR: 0.71, TD: 14.5 ms) and OOI (NF: 6.1 Hz, DR: 0.68, TD: 15.6 ms) showed roughly similar characteristics in eight subjects. The dynamics in the tongue (generated by combined muscles) also showed similar characteristics (NF: 6.1 Hz, DR: 0.68, TD: 17.4 ms) in two subjects. The NF was higher, and the DR was lower than results measured for arm muscles (NF: 4.25 Hz, DR: 1.05, TD: 23.8 ms for triceps long head), indicating that articulatory organs adapt for more rapid movement. In contrast, slower response dynamics was estimated when muscle force data by voluntarily contraction task were used for force-generation dynamics modeling. We discuss methodological problems in estimating muscle dynamics when different kinds of muscle contraction methods are used.

electrical stimulation; lip; muscle model; parameter identification

FORCE GENERATED BY THE SPEECH articulator muscles is precisely regulated by the central nervous system (CNS), generating movements that produce smooth and natural speech. This force is not instantaneously produced by a command from the CNS because of the delay in muscle mechanochemical dynamics. The CNS thus takes the delay into account when producing motor commands for the articulators. To better understand the mechanism of speech articulator movement and its control, we need to characterize the muscle dynamics of speech articulators.

Mannard and Stein (19) concisely modeled the force-generation dynamics of a cat's soleus muscle as a second-order filter with a time delay (TD). Although each muscle has complex characteristics, such as catchlike effects (8), this model has been frequently used for muscle force estimation to reconstruct human arm motion in a musculoskeletal model (18, 21) and for the development of a functional electrical stimulation system for aiding paralyzed limbs (2). One of the advantages of the concise model is that it can easily capture the dynamic characteristics of muscle contraction.

Studies that have used the concise model have shown that the natural frequency (NF), which dominates system delay, differs depending on the body part [1.73 Hz in finger (Ref. 2), 2.05 Hz in limb (Ref. 18), and 3 Hz in jaw (Ref. 9)]. Baratta and Solomonow (3) showed, using an identical method, that frequency responses significantly differ between the nine different muscles of a cat's limb. Speech articulators require relatively rapid movement [∼6 Hz for repetitive lip movement, as shown in Kelso et al. (16) and in our analysis in this paper] compared with limb movement. Additionally, articulatory organs can quickly generate compensatory movements when an external disturbance is suddenly applied to them (1, 12). It is therefore likely that articulator muscles have faster force-generation dynamics than the human muscles previously investigated (2, 18).

In this study, we investigate the force-generation dynamics of speech articulators, the lips [orbicularis oris superior (OOS) and inferior (OOI)], to determine how quickly articulator muscles respond for actively regulating speech movements. First, we characterize the lips as a linear second-order model, with TD from force signals being induced by pulsatile electrical stimulation of the corresponding motor nerves. Next, we compare the estimated parameters with those for limbs to confirm whether the lip muscles have fast force-generation dynamics. Additionally, we apply the same method to the tongue to estimate the dynamics of tongue muscles. Finally, we compare the response characteristics of OOS and OOI muscles obtained by two muscle-contraction methods: one that uses the single pulsatile electrical stimulation and one that uses voluntary contraction task. From the present and previous observations, we discuss methodological differences for estimating the force-generation dynamics.

METHODS

Subjects and Data Recording

Different groups of subjects participated in each experiment. The numbers of subjects are shown in Table 1. Seven of those who participated in the OOS experiment also participated in the OOI experiment. Four of those also participated in the arm experiment

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Table 1. *Identified force-generation dynamics parameters, cutoff frequency, and number of subjects who participated in each experiment*

Muscle	NF(ω_n), Hz	DR (ζ)	TD (τ), ms	CF, Hz	*n*
Electrical stimulation experiment					
OOS	6.10 (0.49)	0.714 (0.036)	14.52 (1.25)	6.04 (0.61)	8
OOI	6.05 (0.46)	0.682 (0.090)	15.55 (1.52)	6.26 (0.93)	8
TNG	6.11 (0.14)	0.675 (0.005)	17.35 (7.00)	6.38 (0.19)	2
TriLo	3.96 (1.04)	1.10 (0.14)	25.03 (1.59)	2.20 (0.27)	4
Voluntary contraction experiment					
OOS	10.94 (9.04)	2.63 (2.34)	22.61 (6.58)	2.91 (2.11)	9
OOI	20.94 (15.62)	8.71 (8.17)	17.33 (8.53)	1.59 (0.76)	9

Values in parentheses are SD among subjects; n = no. of subjects. CF, cutoff frequency, which is the lower frequency bound for gains than −3 dB; DR, damping ratio; NF, natural frequency; OOS, orbicularis oris superior; OOI, orbicularis oris inferior; TD, time delay; TNG, tongue; TriLo, triceps long head.

(triceps long head group; TriLo), and two of those also participated in the tongue experiment (TNG group). In the experiment of voluntary contraction, there were nine subjects. Seven of these participated in the OOS experiment that used electrical stimulation, and eight participated in the OOI experiment. All subjects had never experienced peripheral neuropathy, and all signed the informed consent form, as approved by the ethical committee of the NTT Communication Science Laboratories.

The experimental setup we used to measure the upper-lip-generated force is shown in Fig. 1*A*. Each subject pressed his or her lip on a cantilever beam, the opposite end of which was attached to a six-axis force sensor (Nitta UFS-3012A15). Unlike limb muscle, the orbicularis oris muscle is interwoven by horizontally and vertically oriented muscle fibers (4, 14). In this experiment, the vertical component of generated muscle force, which could produce a vertical motion, was recorded (2 kHz sampling). The experimental setup considerably restricted lip motion. The subject's head was strapped to a headrest to prevent head movement, and the subject was additionally asked to keep the teeth clenched or bite a plastic block to suppress any contribution of jaw movement during the lower-lip force-generation task.

In TNG experiments, the tongue body was maintained almost completely in a rest position on the mandible (to allow no contraction). The mouth was held slightly open so as to make a space in the oral cavity for the cantilever beam (Fig. 1*A*) and the electrode bar. The dorsum of the tongue lightly pressed against the beam. The translational forces in three dimensions could be directly measured with the force sensor because of the rigid beam. The principally acting directions of the tongue force in three dimensions were reproduced off-line from the recorded force signals with the use of a principal component analysis, in which the eigenvalue and eigenvector were calculated with a covariance matrix of the measured force signals. In the electrically induced response, the fastest component was extracted as the tongue force response for parameter identification.

In the TriLo experiments, the rotational force generated horizontally by the right forearm was measured by using the setup shown in Fig. 1*B*. Each subject maintained a particular posture on the horizontal plane (Fig. 1*B*). A six-axis force sensor (Nitta UFS-3012A15), which was attached to the beam supporting the forearm, was set beneath the elbow joint, and the joint rotational center was aligned with the center of the force sensor. The subject's wrist joint was tightly strapped to the beam supporting the forearm. This setting considerably restricted a rotation of the forearm.

The EMG activities were measured with Ag/AgCl surface bipolar electrodes. We amplified and filtered the EMG signals using a biomedical amplifier with a 50- to 1,500-Hz band-pass filter (Nihon Kohden MME-3116); these were recorded at 24 kHz using an analog-to-digital converter (PAVEC DF-2022Z). In lip muscle experiments, the EMG signals of the ipsilateral muscles (OOS and OOI) and depressor anguli oris and mixed activity of the upper lip elevation muscles (zygomatic major, zygomatic minor, levator labii superiors, and levator anguli oris) for the corresponding stimulus site were measured. In the arm experiment, the EMGs of the triceps long head and lateral head, biceps, and brachioradialis were measured. The EMG signals of the tongue muscles were not measured because of the difficulty of measuring them with a surface electrode.

Force-Generation Dynamics Model

Although muscle dynamics have complex mechanisms (28, 29), researchers have had some success in representing the relationship between muscle force and EMG signals in humans [finger: Akazawa et al. (2), arm: Koike and Kawato (18), jaw: Cooker et al. (9)] and in cats [limb: Mannard and Stein (19) and Baratta and Solomonow (3)] using a second-order dynamics with a TD such as

$$\mathrm{D}(s) = \frac{G\omega_n^2}{s^2 + 2\zeta\omega_n s + \omega_n^2} e^{-\tau s} \tag{1}$$

where ω_n denotes NF, ζ denotes the damping ratio (DR), τ denotes the TD, G denotes the gain, and s is a Laplacian operator. We refer to this D(s) as the "force generation dynamics model."

From a physiological perspective, this model can be interpreted to mean that the second-order dynamics represents a chemical dynamics for the variation of calcium concentration in muscle fiber and a

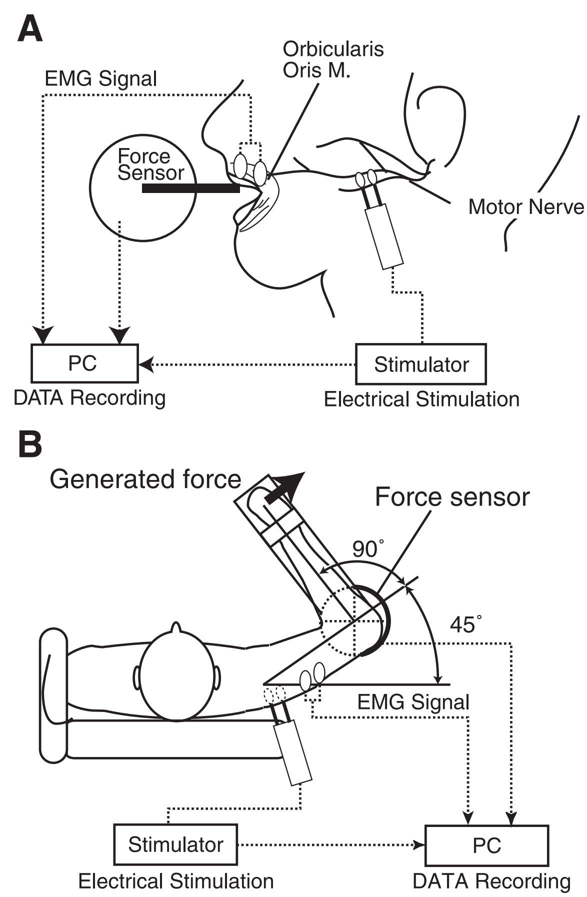

Fig. 1. *A*: setup for testing force generation by electrical stimulation of orbicularis oris superior (OOS) and for the 2 other muscles [orbicularis oris inferior (OOI) and tongue]. *B*: setup for testing force generation by electrical stimulation of arm muscle [triceps long head (TriLo)]. M, muscle.

mechanical dynamics for sliding filament (6, 29) and that TD represents the neural transmission delay (19) and the chemical transmission delay of muscle contraction (5, 23).

The relationship between muscle force [F(t)] and EMG signal (rectified and smoothed) [E(t)] can be represented as

$$F(t) = D(s)E(t) \tag{2}$$

The temporal variation in muscle force, F(t), can be reproduced from the corresponding EMG signal, E(t), if the model, D(s), can identify the actual force generation dynamics of a particular muscle.

Identification Using Electrically Induced Muscle Force

Electrical stimulation. To obtain the muscle activation impulse response, we induced a low level of muscle contraction by electrically stimulating the motor nerves. During the electrical stimulation, the subjects were instructed to maintain a relaxed posture. One hundred responses were obtained for the parameter estimation, which is explained later.

The pulse stimulus signal (300-μs duration) was generated with an electrical stimulator (Nihon Kohden SEN-3301) and isolator (Nihon Kohden SS-104J) every 500 ms (OOS, OOI, and TNG groups) or 750 ms (TriLo group). We confirmed that the force response with these intervals was the same as that with longer intervals. The stimulus intensities for the lips and arm were set for each subject at a painless level, which were three or four times higher than the corresponding sensory threshold level (minimum level to be able to feel the stimulus input). The sensory threshold level was measured at the beginning of the experiment for each subject. To suppress any pain from the stimulation of the tongue, the subject's tongue was topically anesthetized with 4% xylocaine administered with a cotton swab around the stimulus site, and the stimulus intensity was set at ~3.0 mA, which is in the range of three or four times the sensory threshold level.

The stimulus site with the largest force response was determined by exhaustively searching the areas under which the corresponding motor nerves were located. The search area for OOS subjects was just beneath the zygomatic bone (~5 cm posterior from the angle of the mouth); for OOI subjects, it was 1 cm above the inferior border of the mandible and ~2 cm posterior from the angle of the mouth. For TriLo group, the search area was the armpit, and, for TNG group, the search area was the inferior surface of the tongue (3 cm posterior from the tongue tip and ~5 mm left of center). Note that the obtained muscle contractions were not by direct stimulation of muscle bundles; this was because the stimulus site was sufficiently far from the measurement site. In TNG experiments, no other site was ever stimulated so that a vagal nerve and/or sensory nerve would not be stimulated. In addition, it is difficult to activate a single tongue muscle by surface stimulation because there might be several kinds of motor nerves innervating different muscle groups around the stimulating spot. Therefore, for TNG experiments, we examined combined force-generation dynamics of several muscles.

The motor nerve was recruited with a pair of surface electrodes [OOS, OOI, and TriLo groups: Nihon Kohden NM-430S (stainless steel), TNG group: specially made electrode (platinum, 0.8 mm in diameter, tips 7 mm apart)]. For TNG experiments, the bipolar electrode is located on the tip of a bar, and the bar is bent at 3 cm from the tip so that the electrode tip can easily access to the stimulus site.

Parameter estimation using nonlinear optimization. Because a pulse stimulus signal was used as the input signal, the obtained force response can be regarded as the impulse response of the force-generation dynamics in *Eq. 1*. The best-fit parameter values were determined by minimizing the sum of the squared error between the measured force and the impulse response of the model by Newton's method. This optimization was actually done with the "lsqcurvefit" function in the MATLAB software (The Mathworks). It should be noted that the initial values of parameters in the optimization process were randomly set within predetermined bounds (ω_n: 1–20 Hz, ζ: 0.3–2.0, τ: 5–40 ms, G: 0.001–10 F_{max}, where F_{max} is maximum force response for each subject). (The term for TD was replaced with a six-order Pade approximation.)

To examine the reliability of the estimated parameters, parameter variations were calculated for 1,000 patterns of averaged force signals, which were derived from 100 trials, based on the bootstrap method (10). Parameter G identified in this estimation was the gain for the electrical stimulation (not for the actual neural input). Because G was affected by the electrical impedance of the skin and other orofacial tissue, it is not discussed here.

Identification of Force-Generation Dynamics by Voluntary Contraction

An alternative method for estimating the force-generation dynamics is to use the data generated by voluntary muscle contraction. This approach has been frequently used in studies of musculoskeletal dynamics (2, 9, 18). To compare the methodological differences, we identified the force-generation dynamics from the muscle force and EMG signal generated by voluntary contraction. We examined this relationship only for the lip muscles (OOS and OOI) because of the clear causal correspondence between the dominantly activated portion and force measurement location, which may be difficult for the tongue.

Voluntary muscle contraction task. The subject positioned his or her lip as shown in Fig. 1*A*. The subject was then asked to sinusoidally and repetitively perform upper lip depression with the guidance of 5-s beeps. Actually, the lip did not move because of the constraining devices. The frequency of the beeps was increased from 1.4 to 4 Hz in each trial. It was difficult for all subjects to consistently generate a lip force beyond a rate of 3 Hz. The subjects monitored the generated force signal to adjust the temporal pattern. Force magnitude was not specified to avoid making the task difficult. For the lower lip muscle, the force and EMG measurements were done in a similar way. Because muscle cannot be individually activated in a voluntary contraction task, several muscles, such as the depressor anguli oris and/or the mentalis, would simultaneously contract. The measured forces would thus include the contribution by other perioral muscles.

Parameter estimation with the least mean squares method. Because the former method cannot be applied because of nonimpulse input, we used the least mean squares method to identify the model parameters of the force-generation dynamics in voluntary contraction. To transform *Eq. 1* represented with the Laplacian operator in the frequency domain to that in the time domain, *Eq. 2* was rewritten as

$$E(t-\tau) = \frac{1}{G}\left[\frac{1}{\omega_n^2}\ddot{F}(t) + \frac{2\zeta}{\omega_n}\dot{F}(t) + F(t)\right] \tag{3}$$

Here, $\ddot{F}$ and $\dot{F}$ denote the second and first time derivatives of F. The TD term in *Eq. 1* is represented as a temporal shift in EMG signal [$E(t)$]. After these parameters are fitted, the EMG signal can be estimated from the measured force signal and its time derivative. The best-fit parameters with the highest correlation coefficient between a measured and estimated EMG signal were determined by exhaustively searching in 0–60 ms of TD. We do not discuss G here because of unknown skin impedance for EMG measurement.

RESULTS

Force-Generation Dynamics of Articulatory Muscles

The thin solid line in Fig. 2*A* shows a typical averaged force response induced by electrical stimulation for the OOS. The force signal rose rapidly ~10 ms after stimulation, peaked at ~50 ms, and returned to its initial state with a slight overshoot. The best-fit impulse response corresponding to the experimental data response (thick dotted line) well fits the observed response (variance accounted for = 0.99). The mean and

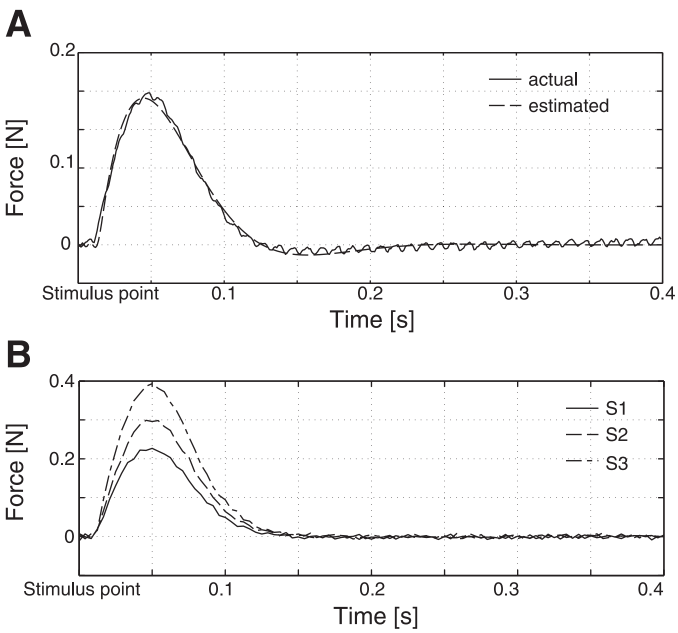

Fig. 2. *A*: measured (solid line) and estimated (dashed line) force responses of the upper lip elicited by electrical stimulation of the motor nerve for one subject. Stimulus start time (stimulus point) is indicated at *left*. Measured force signal is the average of 100 trials; estimated force response was derived from the impulse response of the muscle dynamics estimated using nonlinear optimization. *B*: force response induced by 3 different intensities (S1, weak; S2, middle; S3, strong) in OOS of one subject.

standard deviation of fitting performance (variance accounted for) for all subjects in each muscles was 0.98 ± 0.018 (OOS group), 0.98 ± 0.019 (OOI group), and 0.98 ± 0.018 (TNG group), respectively.

The identified parameter values (ω_n, ζ, and τ) in *Eq. 1* are shown in Table 1. For the lip muscles (OOS and OOI), the corresponding values were not statistically different by *t*-test ($P > 0.1$). This suggests that the orbicularis oris muscle has a homogeneous property in terms of force-generation dynamics.

The parameter values obtained for the tongue (Table 1) were close to those for the lips. Note that a visual inspection before force measurements revealed that the stimulation caused large movement of the dorsum of the tongue (~5 mm left of center and ~3 cm posterior from the tip) in the ipsilateral part of the stimulus site. According to off-line analysis for the generated force direction, in one subject, the dominant force was generated to the right and upward; in another, it was to the left and upward. The reason for this difference was the experimental difficulty in stimulating the particular nerve innervating the same muscles in both subjects. We conjectured that a part of genioglossus, one of extrinsic muscles, was mainly activated. Although the identified parameters cannot specify the characteristics of a single muscle in the tongue, this result suggests that the tongue also has fast dynamics that allow it to quickly configure a complicated shape during speech production and other lingual movements.

To examine the effect of stimulus intensity, we checked the force response of different stimulus intensities for the OOS muscle of the four subjects. The magnitude of the response increased with intensity, whereas the temporal pattern of the response was barely affected, as shown in Fig. 2*B* (one subject). Initial peak values of this force signal [0.236 ± 0.0054 (SD) N for weak intensity, 0.306 ± 0.0093 (SD) N for middle intensity, and 0.396 ± 0.0047 (SD) N for strong intensity] were significantly different by ANOVA ($P < 0.05$). The identified parameters (NF, DR, and TD) were very similar among these responses, and the maximum parameter variations among the four subjects were less than 4.0% (NF), 7.6% (DR), and 4.7% (TD) of the corresponding values (OOS) in Table 1. This result suggests that stimulus intensity affects the frequency property less with this method.

Frequency responses for the OOS, OOI, and TNG groups are shown in Fig. 3. The gain curves did not decrease up to ~6 Hz. The cutoff frequency (CF), which is the lower frequency bound for gains less than −3 dB, was 6.04 ± 0.61 (SD) Hz (OOS group), 6.26 ± 0.93 (SD) Hz (OOI group), and 6.38 ± 0.19 (SD) Hz (TNG group).

Comparison With Force-Generation Dynamics of Arm Muscle

To clarify the muscle difference in force-generation dynamics, we performed the same estimation for the arm muscle. The parameter values obtained for the arm muscle shown in Table 1 were significantly different ($P < 0.05$ by *t*-test) from those for the articulatory muscles. These differences account for the large difference in the gain curves in Fig. 3. The gain for the arm muscle started decreasing at a lower frequency than that for the articulators. Moreover, CF of the gain response for the arm (2.20 ± 0.27 Hz) was significantly lower than that for the lips ($P < 0.05$ by *t*-test), indicating that the articulatory muscles react more rapidly to motor commands than the arm muscles.

DR in force-generation dynamics was assumed as critically damped ($\zeta = 1$) in previous studies (3, 9, 19). Our results for the arm muscle agree with that assumption, as shown in Table

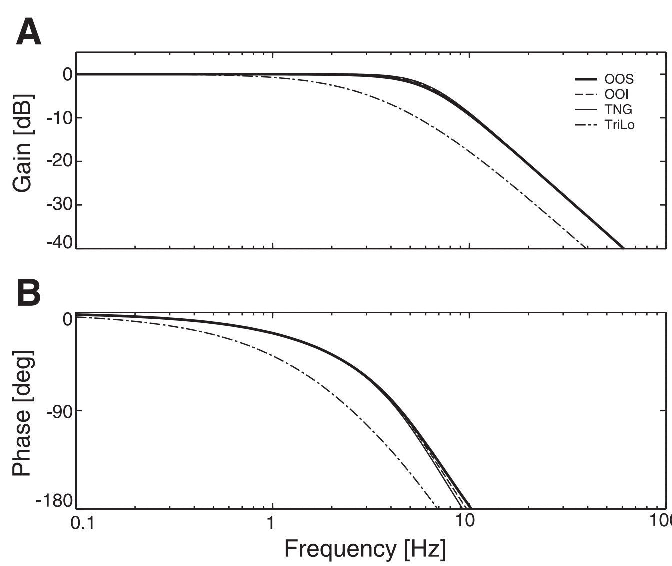

Fig. 3. Frequency responses of identified force-generation dynamics [thick line, OOS; broken line, OOI; thin line, tongue group (TNG); dashed line, TriLo]. In the gain diagram (*A*), responses of 3 articulatory muscles (OOS, OOI, and TNG) are superimposed. The frequency at which the response of TriLo starts decreasing is lower than that at which the others do. *B*: phase diagram of the corresponding gain function.

1. In contrast, the DRs of the articulatory muscles were significantly <1 ($P < 0.001$ by t-test). Because of this low DR, the force response of articulatory muscles can immediately converge, as shown in Fig. 2*A*. This property might be inherent in articulatory muscles performing sequential tasks with quick movements, such as speech.

Lip Muscle Dynamics Identified by Using Voluntary Contraction Task

For comparison, we also obtained the force-generation dynamics identified by using the repetitive voluntary contraction task. As shown in the bottom two rows of Table 1, the value of the identified parameters differed significantly ($P < 0.01$ by t-test) when the voluntary contraction data were used. They were also significantly different ($P < 0.01$) in the paired t-test for the same subjects ($n = 7$ for OOS group, $n = 8$ for OOI group).

As a result, the frequency responses differed considerably between electrical stimulation and voluntary contraction, as shown in Fig. 4. The CFs for the voluntary contraction were 2.91 ± 2.11 Hz (OOS group) and 1.59 ± 0.76 Hz (OOI group). This indicates that rapid movement is difficult to generate by the quick change of muscle activation, which contradicts the observation of articulatory movement (16, 27). Thus the voluntary contraction method is barely adequate to represent the muscle dynamics, especially for generating a fast movement over 3 Hz.

In addition to the differences in model parameter values, parameter variabilities of NF, DR, and TD were also different from those of the electrical stimulation method (Table 1). This may be mainly due to the variability of low-frequency component in the measured data among subjects. Figure 5 shows that, with the voluntary contraction method, the magnitude of the power spectrum of force responses at ~3–5 Hz having high gain varied according to the task performed by each subject. In contrast, such variability was not shown in the low-frequency range (<8 Hz) of force response induced by the electrical stimulations (see thick solid line in Fig. 5). Because the input variability in the voluntary condition affected parameter estimation, the voluntary contraction method would not be suitable to use for estimating lip muscle dynamics during speech.

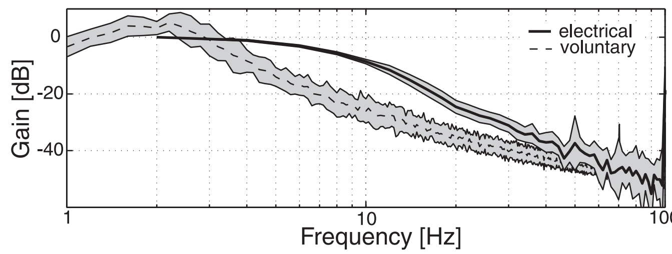

Fig. 5. Averaged power spectrum of generated force signal in OOS muscle (7 subjects participated in both experiments). Gray areas represent the SD among subjects. In frequency range over 3 Hz, the power spectrum gain in voluntary contraction method was considerably lower than that in electrical stimulation method.

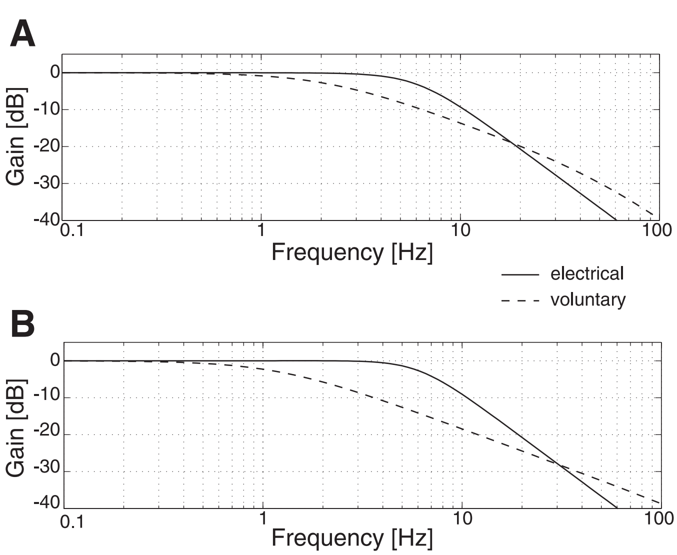

Fig. 4. *A*: gain diagram of identified force generation dynamics from electrically and voluntarily induced forces for OOS. *B*: gain diagram for OOI.

DISCUSSION

Muscle Differences in Force-Generation Dynamics

Force-generation dynamics has been investigated for several muscles in humans (2, 9, 18) and in cats (3, 19). The identified dynamics in these studies differs considerably, as shown by the frequency responses in Fig. 6. Actually, the lip muscle dynamics studied here had the highest NF. Because of methodological differences in driving muscles, however, we cannot simply ascribe these differences to differences in muscle characteristics.

To rigorously consider the muscle difference, we compared the force-generation dynamics of the lip, tongue, and arm identified using the force responses driven by an identical method: single pulsatile electrical stimulations to the nerves

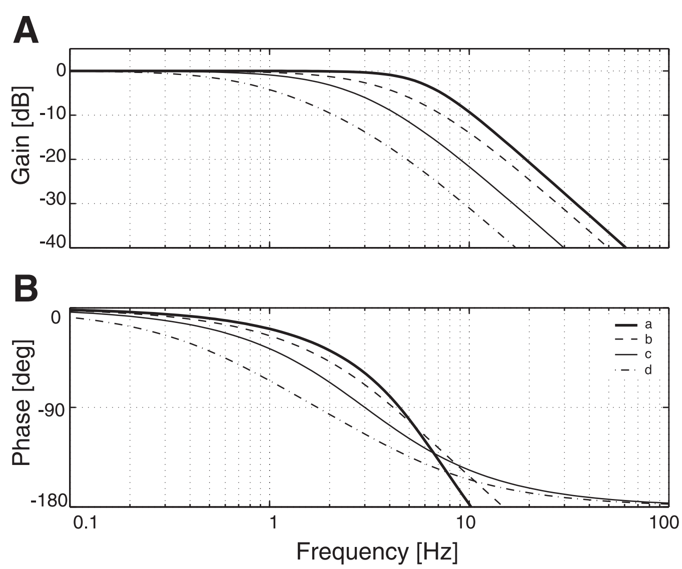

Fig. 6. Gain (*A*) and phase diagram (*B*) of force-generation dynamics. *Line a*: our estimated dynamics of OOS. Natural frequency (NF) = 6.10 Hz; damping ratio (DR) = 0.714; time delay (TD) = 14.52 ms. *Line b*: frequency response from Mannard and Stein (19). NF = 5 Hz; critically damped; TD = 7 ms. *Line c*: frequency response from Cooker et al. (9). NF = 3 Hz; critically damped; no TD. *Line d*: frequency response from Akazawa et al. (2). NF = 1.73 Hz; DR = 1.29; no TD.

innervating the target muscles. We found that the dynamics of articulatory muscles is quite similar when compared with each other; however, the dynamics of the arm muscle differ significantly from that of the articulators. One potential reason for this discrepancy is that large muscles could not respond as rapidly as small facial muscles. However, this contradicts the results of Baratta and Solomonow (3), who showed that the force-generation dynamics for nine different muscles of a cat limb do not correlate with muscle length.

Another possible explanation for the difference in force-generation dynamics is biomechanical characteristics. The force generated by the lips and tongue muscles could directly transmit to the force sensor because of the lack of skeletal support, which is known as a muscular hydrostat system (17). On the other hand, in the limb system, the tendon, joint, and considerable mass intervene between muscle fibers (force-generation point) and skeletal links (force-measurement point). When the forearm is tightly constrained, as it was in our experiment, joint and mass effect would have little influence on the force measurement. According to Zajac (29), the tendon of the upper limb is highly stiff. In addition, the human finger muscle, which has a long tendon organ, has a fast contraction time (45.9 $\pm$ 4.5 ms) in a particular subject group (11), which is comparable to Buchthal and Schmalbruch (7) and to the identified arm muscle dynamics in the present study. These observations suggest that the tendon system also has less influence on the force measurement. However, we cannot completely rule out the contribution of tendon elasticity to the slow-force response because of the serial connection of muscle and tendon. Clarifying this issue will require direct measurement of tendon stiffness.

A muscle's histological property might partly explain the difference in force-generation dynamics. A muscle fiber can be generally classified into two types (slow twitch and fast twitch) according to its contraction speed. These types correspond to classification by staining (type I and II). Buchthal and Schmalbruch (7) found that nearly all fibers in arm triceps muscles are fast-twitch muscle fiber (type II), based on muscle contraction speed (44.5 $\pm$ 9.5 ms) and histochemical results. On the other hand, the orbicularis oris muscle (24, 25) and intrinsic tongue muscle (26) consist of type I and II in roughly equal proportions. This means that the articulatory muscles have a high NF despite having fewer fast-twitch fibers (type II) than arm muscles. However, human jaw muscles and extraocular muscles contain a specific "superfast" myosin (28). Although the masseter muscle predominantly consists of type I fibers, as shown by staining, its contraction is very fast (mean of 34 ms) (20). Thus, in a particular muscle, classification by conventional staining is not fully compatible with the differences in the muscle's physiological properties.

We therefore infer that force-generation dynamics might adapt functionally for each muscle. For example, an organ requiring quick movement, such as an articulator, would have a muscle that can contract rapidly at an appropriate speed. Further investigation is required to clarify this point.

Difference in Muscle Contraction Methods

As shown in RESULTS, force-generation dynamics differed according to muscle contraction methods for the same muscle (OOS and OOI, respectively). Compared with previous studies, the pulsatile electrical stimulation method (Ref. 19 and our dynamics of OOS in Fig. 6) could estimate the dynamics with high NF. In limb muscle, the NF of our dynamics (3.96 Hz) was approximately two times higher than that of other studies [1.73 Hz: Akazawa et al. (2), 2.05 Hz: Koike and Kawato (18)]. Baratta and Solomonow (3) obtained a low NF (1.8 Hz) by using repetitive electrical stimulation to a cat soleus muscle, whereas higher NF (5 Hz) was obtained by using a single pulsatile electrical stimulation (19). They pointed out that the single pulsatile stimulation can fully activate a muscle at all times and suggested that the identified force-generation dynamics may depend on the pattern of the stimulus input.

The CNS can selectively activate the motor unit (29), for example, according to the size principle (13), to generate a desired net muscle force for a particular movement. Although it is difficult to know how the CNS recruits the motor units according to motor tasks, it could be possible that it recruits motor units of the fast-twitch fibers when quick movement is required. The pulsatile stimulus of Mannard and Stein (19) might be a reasonable way to identify the upper bound of the response of the force-generation dynamics in a particular muscle because of full activation of the muscle fibers. The force-frequency response obtained by electrical stimulation in this study (solid line in Fig. 5) started decreasing at ~6 Hz. This frequency property might reasonably produce a fast articulatory movement [for the production of bilabial consonants, the lip moved 6 Hz (16) or up to 8 Hz in an unpublished analysis based on the data of Gomi et al. (12)] and quick lip motion [the lip moved from unrounded to rounded in the 50- to 100-ms range (Ref. 27)]. Our pulsatile electrical stimulation method may be useful for characterizing the fast force response of articulator muscles.

In contrast, a low-frequency response (e.g., low CF) was obtained by the voluntary contraction method, which is also in accord with a previous study (22). In our voluntary contraction experiment, it was difficult for subjects to generate lip muscle force at a frequency of >3 Hz, as noted in METHODS. This is mainly owing to the contribution of the motor units with slow-twitch fiber in voluntary contraction. Although Cooker et al. (9) used the force and EMG data produced by tremors in a frequency range that exceeded the limit of voluntary contraction in estimating muscle dynamics, the NF of the identified dynamics was low (3 Hz), as in other studies that used voluntary contraction methods (2, 18). These results might indicate that it is difficult to dominantly activate fast-twitch muscle fibers in generating forces in isometric voluntary contraction tasks, although those fibers might be momentarily activated to generate a quick phase of continuous normal motion. Consequently, the identified dynamics would be restricted by a particular isometric contraction task. The electrical stimulation method can overcome this limitation and thereby allow us to estimate the upper bound of the muscle force-generation dynamics for various movements.

Nonlinearity of Force-Generation Dynamics

Although force-generation dynamics has been concisely represented as a linear second-order model with a TD in the present and previous studies, a more complicated model is needed to represent the nonlinear properties of muscle contraction. To predict the force in response to an arbitrary pulse train, Bobet et al. (6) proposed a quasi-linear model with time-varying parameters. Otazu et al. (23) represented the nonlinear characteristics of muscle, such as the catchlike effect (8), by modeling in detail the chemical dynamics. However, these models require many parameters, which are not easy to determine from behavioral experiments.

Force has been successfully estimated with linear models with or without a TD (2, 18, 21), indicating that such models approximate the force-generation dynamics under particular conditions. In addition, we demonstrated that the force impulse responses of the orofacial muscles in this fits nicely and showed the quick response characteristics of these muscles. The identified parameters of force-generation dynamics will be helpful in producing an articulatory model (15) and investigating the speech motor control mechanism.

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