Fast force-generation dynamics of human articular muscles

Takayuki Ito, Emi Z. Murano, and Hiroaki Gomi

NTT Communication Science Laboratories, Nippon Telegraph and Telephone Corporation, Kanagawa 243-0198; ATR Human Information Science Laboratories, Kyoto 619-0288; and Interdisciplinary Graduate School of Science and Engineering, Tokyo Institute of Technology, Kanagawa 226-8502, Japan

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HIGHLIGHTED TOPIC | Neural Control of Movement

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Fig. 1

Tally by the right forearm was measured by using the setup shown in the tongue force response for parameter identi- electrically induced response, the fastest component was extracted as with a covariance matrix of the measured force signals. In the analysis, in which the eigenvalue and eigenvector were calculated force sensor because of the rigid beam. The principally acting direc- dorsum of the tongue lightly pressed against the beam. The transla-

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

<table>
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<tr>
<th>Muscle</th>
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<td>OOS</td>
<td>6.10 (0.49)</td>
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<td>OOI</td>
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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, cutoff frequency; 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 par-

In the TriLo experiments, the rotational force generated horizon-

tally by the right forearm was measured by using the setup shown in

A

EMG Signal

Orcicularis Oris M.

Stimulator

PC

DATA Recording

Electrical Stimulation

B

Generated force

Stimulator

PC

DATA Recording

Electrical Stimulation

45°

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.

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Electrical stimulation experiment

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... 1992. Finally, the EMGs of the OOS and OOI were filtered using a 30- 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

\[
D(s) = \frac{G_0\omega_n^2}{s^2 + 2\xi\omega_n s + \omega_n^2} e^{-\zeta s}
\]

where \(\omega_n\) denotes NF, \(\xi\) denotes the damping ratio (DR), \(\tau\) 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...
mechanical dynamics for sliding filament (6, 29) and that TD repre-
sents 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

\[
F(t) = D(s)E(t)
\]  
(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 contraction 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
was asked to sound a low
pitched tone when the
stimulus was perceived.

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
subjects, 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 measure-
ment 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-4305 (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 “lscurvefit”
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 (\( \omega_n \): 1–20 Hz, \( \zeta \):
0.3–2.0, \( \tau \): 5–40 ms, G: 0.001–10 \( F_{\text{max}} \), where \( F_{\text{max}} \) is maximum force
response for each subject). (The term for TD was replaced with a
six-order Padé approximation.)

To examine the reliability of the estimated parameters, parameter
variations were calculated for 1,000 patterns of averaged force sig-
als, 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 dynam-
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. 1A. 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
device. 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 trans-
form Eq. 1 represented with the Laplacian operator in the frequency
domain to that in the time domain, Eq. 2 was rewritten as

\[
E(t - \tau) = \frac{1}{G} \left( \frac{1}{\omega_n} \tilde{F}(t) + \frac{1}{\omega_p} \tilde{F}(t) + F(t) \right)
\]  
(3)

Here, \( \tilde{F} \) and \( F \) denote the second and first time derivatives of \( F \). The
TD term in Eq. 1 represents 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. 2A 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 experimen-
tal data response (thick dotted line) well fits the observed
response (variance accounted for = 0.99). The mean and
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 ($\omega_n$, $\zeta$, and $\tau$) 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. 2B (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.
In contrast, the DRs of the articulatory muscles were significantly < 1 \( (P < 0.001 \ \text{by} \ \text{t-test}) \). Because of this low DR, the force response of articulatory muscles can immediately converge, as shown in Fig. 2A. 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 \( (P < 0.01 \ \text{by} \ \text{t-test}) \) when the voluntary contraction data were used. They were also significantly different \( (P < 0.01) \) in the paired \( t \)-test for the same subjects \( (n = 7 \ \text{for OOS group,} \ n = 8 \ \text{for OOI group}) \).

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 \( \sim 3–5 \) 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.

**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...
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 hydrosstat 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 ± 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 ± 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 articular 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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REFERENCES