Excitatory and Inhibitory Controls of the Masseter and Temporal Muscles Elicited from Teeth in the Rat

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Abstract  The periodontal mechanism that controls the jaw reflexes was examined in lightly anesthetized rats. Motor-unit activity in the masseter and temporal muscles was recorded electromyographically and pressure stimulation was applied to either an upper incisor or an upper molar. Reflex effects of dental stimulation varied depending on the level of ongoing activity (background activity, BGA) in each motor unit. Incisal or molar stimulation elicited excitatory reflexes in both the masseter and temporal motor units at a low BGA, but inhibitory reflexes in both types of motor unit at a higher BGA. In contrast to these synergistic reflex actions, the reciprocal reflex actions of the two motor units that belonged to the respective muscles occurred when the BGA was intermediate. The results suggest that different patterns of periodontal jaw reflexes may be elicited, depending on the different levels of BGAs. Furthermore, the present reflexes were modified with the site of a stimulated tooth within the dentition. Incisal stimulation produced greater excitation in the masseter motor unit than in the temporal one, and the opposite type of response occurred during molar stimulation. Moreover, smaller-amplitude motor units with a low reflex threshold and larger-amplitude motor units with a higher reflex threshold tended to exhibit excitatory and inhibitory reflexes, respectively.

Key words: periodontal jaw reflex, masseter and temporal muscles, incisor and molar, background activity.

In spontaneous movements of the jaw, the patterns of activity of each jaw-closing muscle are determined by the occlusal position. For example, while the masseter muscle is more active than the temporal muscle during occlusion of the incisor teeth in humans and rats, both muscles are equally active during molar occlusion [1–3]. These patterns of activity of the muscles are efficient, as judged from the running directions of the muscle fibers [4, 5]. However, the way in which reflex regulation acts on each muscle in an integrated manner remains unknown.

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There are several previous reports about reflex regulation of individual jaw-
closing muscles, demonstrating that mechanical stimulation of a tooth induces
excitatory or inhibitory responses with respect to the activity of the jaw-closing
muscles in cats, humans, rats, and rabbits [6–13]. However, the integrated reflex
effects on the jaw-closing muscles and conditions for determining an excitatory or
an inhibitory reflex have not been reported.

The present report is concerned with integrated reflex effects on the masseter
and temporal muscles and with the role of afferent information from an incisor or
a molar in modulating the activity of the jaw-closing muscles in the rat. Furt-
hermore, the role of ongoing motor-unit activity, the site of a stimulated tooth
within the dentition, and the amplitude of motor units were considered in an
investigation of factors that influence reflex effects.

MATERIALS AND METHODS

Twenty-four Wistar albino rats (male and female, 280–580 g body weight)
were used. The rats were anesthetized with intraperitoneally administered α-
chloralose (40 mg/kg) and urethane (500 mg/kg). Each was placed in a supine
position with its head fixed by a pair of ear rods, and the trachea was cannulated.
The body temperature was maintained at about 37°C by a thermostatically con-
trolled heating pad. The mandible was pulled upward with a ligature wire and the
mouth was opened to give a distance of about 10 mm between the upper and lower
incisors.

Bipolar concentric wire electrodes (50 μm in diameter, enamel-coated) were
inserted unilaterally into the right anterior superficial masseter and right anterior
temporal muscles. The position of the electrodes in the muscles was adjusted to
produce a stable recording of motor-unit activity with a good signal-to-noise ratio.
In order to maintain a long-term recording from the same motor unit, the inserted
portion of the electrodes was fixed to the muscles by dental cyano-acrylic adhesive.
The recordings from the same motor unit were continued until the end of a given
experimental session, and quantitative analyses of the results were then performed.
The action potentials were amplified by a conventional amplifier, displayed on an
oscilloscope, and recorded with a pen-driven oscillograph.

By means of a plastic probe connected to an electromechanical transducer, a
pressure stimulus with a duration of about 2 s was applied manually to the right
upper incisor in the lingolabial direction and to the right upper first molar in the
axial direction, imitating the working directions of the bite force during natural
chewing. The intensity of the pressure stimulus was about 300 g, which corresponds
to the average bite force during natural chewing [14].

Stimulation was applied during recordings from motor units with varying
background activities (BGAs). To induce different BGAs in the masseter muscle
before stimulation, weak mechanical stimuli to a lower incisor in labiolingual
direction and that to the anterior parts of the oral mucous membrane, such as the

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incisive papillae, were effective. In order to induce BGAs in the temporal muscle, successive weak mechanical stimuli were applied to a molar or to the surrounding gingiva or buccal mucosa. With a combination of these methods, BGAs could be simultaneously induced in both the masseter and temporal muscles. Different levels of BGAs were obtained by changing the intensity of the stimulus.

Reflex responses of the masseter and temporal motor units were analyzed quantitatively at different levels of BGA from 0 to 80 Hz. The firing rate of a motor unit for 1 s prior to stimulation was compared with that during 1 s of steady-state firing during stimulation, with the phasic "on" and "off" responses omitted. When the firing rate was increased or decreased during stimulation, excitatory or inhibitory reflexes, respectively, were judged to have been induced.

RESULTS

The reflex responses of motor units in the masseter and temporal muscles were recorded while an incisor or a molar was stimulated mechanically. The threshold pressures for the masseteric excitatory and inhibitory reflexes were less than 10 g for incisal stimulation and more than 100 g for molar stimulation. The threshold pressure for the temporal muscle reflex was about 50 g, higher than that for the masseter muscle. The threshold for excitatory reflexes increased with an increase in the BGA, whereas the threshold for inhibitory reflexes decreased with an increase in the BGA. Both excitatory and inhibitory reflex thresholds decreased gradually when successive stimulation was applied every few seconds.

Excitatory and inhibitory reflexes that depend on the background activity

With incisal stimulation, excitatory and inhibitory reflexes appeared at relatively low and relatively high BGAs, respectively, in the masseter and temporal muscles. At a low BGA, the motor-unit activity in the masseter and temporal muscles increased from 38 to 60 Hz (Fig. 1A) and from 22 to 36 Hz (Fig. 1B), respectively, during incisal stimulation. At a higher BGA, the motor-unit activity in the masseter muscle disappeared at 47 Hz (Fig. 1C) as did that in the temporal muscle at 35 Hz (Fig. 1D). In most cases, inhibition at a higher BGA was so intense that the muscle activity was completely suppressed during the period of stimulation.

Reflex responses that depended on the BGA were also induced by molar stimulation. At a low BGA, the motor-unit activity in the masseter and temporal muscles increased from 0 to 21 Hz (Fig. 2A) and from 38 to 57 Hz (Fig. 2B), respectively. At a higher BGA, the motor-unit activity in the masseter muscle disappeared at 30 Hz (Fig. 2C), while that in the temporal muscle decreased slightly, falling from 58 to 55 Hz (Fig. 2D). Clear inhibitory reflexes could not be induced in the temporal motor unit (Fig. 2D), but strong inhibitory reflexes could be induced in the masseter motor unit (Fig. 2C). The masseter and temporal motor units responded with different firing rates to periodontal stimulation. The motor
Fig. 1. Electromyographic responses of masseter and temporal motor units to incisal stimulation. Upper traces in A–D show motor-unit activity (EMG) and lower traces show stimulation by lingolabial pressure of an upper incisor with a load of about 300 g. Excitatory and inhibitory reflexes were induced during pressure stimulation at low (A, 38 Hz; B, 22 Hz) and higher (C, 47 Hz; D, 35 Hz) BGA, respectively. M.EMG, masseter electromyogram; T.EMG, temporal electromyogram; Stim., stimulus.

Fig. 2. Electromyographic responses of masseter and temporal motor units to molar stimulation. Upper traces in A–D show motor-unit activity (EMG) and lower traces show axial pressure stimulation of an upper molar with a load of about 300 g. The motor units for the recordings in A and B were the same as those in C and D, respectively. Excitatory and inhibitory reflexes were induced during pressure stimulation at low (A, 0; B, 38 Hz) and higher (C, 30 Hz; D, 58 Hz) BGA, respectively. Abbreviations as in Fig. 1.
units from which the recordings shown in Fig. 2A and B were made were the same, respectively, as those from which recordings in Fig. 2C and D were made. Even in the same motor unit, the reflex response to dental stimulation varied, depending on the level of the BGA. This phenomenon was consistently reproducible in all motor units tested.

Quantitative analyses of reflex responses elicited from an incisor and a molar

Figure 3A shows the reflex effects on the masseter and temporal motor units recorded when stimulation by lingolabial pressure was delivered to an upper incisor. The positive and negative values along the Y-axis represent the increase and the

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![Graph A](image)

**Graph A** shows the reflex responses induced by pressure stimulation (300 g) of an upper incisor (A) and an upper molar (B). The positive and negative values along the Y-axis represent the magnitude of the increase and decrease in the firing rates, respectively, of the motor unit in response to dental stimulation. The open and filled circles in the graph were obtained from the same masseter and temporal motor units, respectively. The reversal level (the BGA when a reflex changed from excitatory to inhibitory) was higher during incisal stimulation in the masseter motor unit than in the temporal motor unit. The reversal level was higher during molar stimulation in the temporal motor unit than in the masseter motor unit.

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decrease in the firing rates, respectively, of the motor unit in response to the stimulation. The open and filled circles on the graph were obtained from the same masseter and temporal motor units, respectively. When the BGAs in the masseter and temporal motor units were low, marked excitatory reflexes were elicited. The magnitude of the excitatory reflexes decreased with an increase in the BGA, and when the BGA was augmented to a significant extent, the motor-unit activity was completely inhibited. The reflex effects of dental stimulation changed, even within the same motor unit and with the same intensity of stimulus, depending on the level of the BGA.

The masseter and temporal motor units responded with different magnitude and threshold values to incisal stimulation. Strong excitatory reflexes were observed in the masseter motor unit, as compared to those in the temporal motor unit. Inhibitory reflexes could more easily be elicited in the temporal motor unit, even at a lower BGA, than in the masseter motor unit.

In Fig. 3A the regression lines corresponding to the open and filled circles are given by the equations: \( Y = 43.39 - 1.07X \), \( r = -0.74 \); and \( Y = 21.95 - 1.08X \), \( r = -0.79 \), respectively. The intersects on the \( X \)-axis were derived and it was clear from the figure that the reflex responses changed from excitatory to inhibitory at a BGA of 40 Hz in the masseter motor unit and at a BGA of 20 Hz in the temporal motor unit. These BGA levels were tentatively designated as the reversal levels of the respective motor-unit activity in the present study.

In all motor units recorded, the reflex responses changed from excitatory to inhibitory depending on the level of the BGA. The reversal levels of several masseter and temporal motor units, taken from data recorded from eight animals subjected to incisal stimulation, are shown in Table 1. The values of reversal levels are distributed over a narrow range. The average values of the reversal levels are 46 ± 1.9 Hz (mean ± SE \( n = 8 \)) and 24 ± 1.5 Hz \( n = 5 \) for the masseter and temporal motor units, respectively. The greater part of the recorded motor units gave an approximately similar value and the remainder gave a lower value.

Figure 3B shows the reflex effects obtained when axial pressure stimulation was delivered to an upper molar. The open and filled circles represent the same as they do in Fig. 3A. The reversal levels in the masseter and temporal motor units were 13 Hz \( Y = 14.77 - 1.13X \), \( r = -0.92 \) and 61 Hz \( Y = 31.56 - 0.52X \), \( r = -0.71 \),

<table>
<thead>
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<th>No. of MU</th>
<th>Mean ± SE</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>RL in the masseter MU (Hz)</td>
<td>40</td>
</tr>
<tr>
<td>RL in the temporal MU (Hz)</td>
<td>20</td>
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</table>

A pair of motor units No. 1 is the same pair of motor units as that for which data are shown in Fig. 3. —, unrecorded.
Table 2. The reversal levels (RL) in the masseter and temporal motor units (MU) induced by molar stimulation.

<table>
<thead>
<tr>
<th>No. of MU</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>Mean±SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>RL in the masseter MU (Hz)</td>
<td>13</td>
<td>18</td>
<td>10</td>
<td>15</td>
<td>23</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>16±2.2</td>
</tr>
<tr>
<td>RL in the temporal MU (Hz)</td>
<td>61</td>
<td>58</td>
<td>50</td>
<td>58</td>
<td>65</td>
<td>58</td>
<td>56</td>
<td>50</td>
<td>57±1.8</td>
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A pair of motor units No. 1 is the same pair of motor units as that for which data are shown in Fig. 3. —, unrecorded.

respectively. The reversal levels of several masseter and temporal motor units, derived from the data recorded from eight animals, are shown in Table 2. The values of the reversal levels are again distributed over a narrow range. The average values of the reversal levels are 16±2.2 (n = 5) and 57±1.8 Hz (n = 8) for the masseter and temporal motor units, respectively. The greater part of the recorded motor units gave an approximately similar value and the remainder gave a lower value. Motor units with higher reversal levels had a smaller spike amplitude and those with lower reversal levels had a larger one.

A regression line could be drawn for every motor unit. More than 90% of the motor units in the same muscle gave similar regression lines when the same tooth was stimulated. However, when a different tooth was stimulated, even the same motor unit gave a different regression line, as exemplified by Fig. 3A and B.

As seen in Tables 1 and 2, the average reversal levels of masseter motor units were 46±1.9 Hz (n = 8) for incisal stimulation and 16±2.2 Hz (n = 5) for molar stimulation. By contrast, the average reversal levels of the temporal motor unit were 24±1.5 Hz (n = 5) for incisal stimulation and 57±1.8 Hz (n = 8) for molar stimulation. Thus, the masseter and temporal motor units seem to be subject to reflex effects of different magnitude as a result of stimulation of the same tooth.

*Reciprocal reflex responses*

Figure 4A shows an excitatory reflex, recorded after incisal stimulation, in a masseter motor unit at a BGA of 50 Hz and an inhibitory reflex in a temporal motor unit at a BGA of 41 Hz. Figure 4B shows the induction of an inhibitory reflex by molar stimulation in the masseter motor unit at a BGA of 50 Hz and an excitatory reflex in the temporal motor unit at a BGA of 58 Hz. These reciprocal reflex responses in the masseter and temporal motor units were also observed in recordings from multiple motor units.

It was clear that the masseter and temporal muscles were controlled not only synergistically but also reciprocally, depending on the change in the BGAs in both muscles. The reciprocal reflex response was observed when the BGA in the motor unit of one muscle was lower than its reversal level, while the BGA in a different motor unit of the other muscle was higher than its reversal level. The reciprocal

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Fig. 4. Reciprocal reflex effects to dental stimulation in the masseter and temporal motor units during simultaneous recordings. Reciprocal reflex responses were induced at intermediate BGAs in motor units of the two muscles because of the difference in the reversal levels. A: During incisal stimulation, an excitatory reflex was elicited in the masseter motor unit (BGA, 50 Hz) and an inhibitory reflex in the temporal motor unit (BGA, 41 Hz). B: During molar stimulation, an inhibitory reflex was elicited in the masseter motor unit (BGA, 50 Hz) and an excitatory reflex in the temporal motor unit (BGA, 58 Hz). Abbreviations as in Fig. 1.

reflex response also appeared when the BGAs in motor units of the two muscles were similar and intermediate.

Reflex responses to motor units with different spike amplitudes

In the present experiment, the activities of several motor units with various spike amplitudes were recorded simultaneously. There was a tendency for the reflex threshold of motor units with a smaller amplitude to be lower than that of units with a larger amplitude. It is known that the amplitude of the spike potential is a function of the size of muscle fibers when it is recorded with bipolar wire electrodes [15]. Recordings were made more frequently from the smaller-amplitude motor units than from the larger-amplitude units.

The reflex responses of the smaller-amplitude and larger-amplitude motor units differed even when their BGAs were similar. Representative responses recorded...
Fig. 5. Differential reflex responses to dental stimulation in smaller-amplitude and larger-amplitude motor units. Excitatory reflexes in a smaller-amplitude motor unit and inhibitory reflexes in a larger-amplitude motor unit were easily induced. A: The activity of the smaller-amplitude motor unit increased from 31 to 69 Hz, whereas that of the larger-amplitude unit was abolished in response to the incisal stimulation while the BGA was kept at 28 Hz. B: Relationship between the BGAs in the two kinds of motor unit and magnitude of reflex responses during stimulation of an incisor. All recordings were made from the same motor unit as that for which data are shown in A. M.EMG, masseter electromyogram; Stim., stimulus.

simultaneously from the same masseter muscle are shown in Fig. 5A. The activity of the smaller-amplitude motor unit increased from 31 to 69 Hz, whereas that of the larger-amplitude unit was abolished in response to the incisal stimulation when the BGA was kept at 28 Hz. The results were analyzed in terms of the relationship between the magnitude of the reflex responses and the BGAs (Fig. 5B).

The smaller-amplitude motor unit having low reflex threshold tended to show an excitatory reflex response but to evoke an inhibitory one at a higher BGA. By contrast, the larger-amplitude unit having a higher reflex threshold tended to show
Fig. 6. Three typical combinations of reflex responses to dental stimulation obtained during simultaneous recordings of smaller-amplitude and larger-amplitude motor units in the masseter and temporal muscles. A: Molar stimulation induced excitatory reflexes in both smaller-amplitude and larger-amplitude motor units of the temporal muscle. B: Incisal stimulation induced inhibitory reflexes in both smaller-amplitude and larger-amplitude motor units of the temporal muscle. C: Molar stimulation resulted in recruitment of larger-amplitude motor units, but caused suppression of the activity of smaller-amplitude motor units in the masseter muscle. These various patterns of reflex responses are explained by differences in reversal levels between motor units. Abbreviations as in Fig. 1.

an inhibitory response but to induce an excitatory one at a lower BGA.

During simultaneous recordings from a smaller-amplitude and a larger-amplitude motor unit in the same muscle, three typical combinations of reflex responses were seen as follows:

Combination pattern 1 (Fig. 6A): activities of both the smaller-amplitude and larger-amplitude temporal motor units were increased by a molar pressure of approximately 400 g. During the stimulation, the activity of the smaller-amplitude unit increased slightly (from 40 to 45 Hz), as compared to that of the larger-amplitude unit which appeared only when the pressure reached the maximum level.

Combination pattern 2 (Fig. 6B): activities of both the smaller-amplitude and
larger-amplitude temporal units were inhibited by a lower pressure of about 200 g on the incisor. The activity of the larger-amplitude unit was abolished at a very low rate of discharge and sooner than that of the smaller-amplitude unit which was abolished at 52 Hz.

Combination pattern 3 (Fig. 6C): inhibitory and excitatory reflex responses were induced in the smaller-amplitude and larger-amplitude masseter units, respectively. The excitatory response was produced only in response to molar pressure of about 300 g in the absence of BGA in the larger-amplitude unit. The smaller-amplitude unit was inhibited at a BGA of 30 Hz, which exceeded its reversal level.

DISCUSSION

Reflex responses vary depending on the background activity. The present study revealed that the reflex effects of dental stimulation varied, even in the same motor unit, depending on the level of the BGA. There are several previous reports demonstrating that the reflex responses of muscles vary with the BGA. Miles and Türker [16,17] applied a mildly noxious electrical stimulus to the human lip and analyzed the magnitude of the muscletic inhibitory reflexes at two levels of pre-stimulus excitability. They showed that the inhibitory responses were larger when the pre-stimulus firing frequency was 10 Hz than when it was 15 Hz. The pre-stimulus firing frequency determined a motor unit's susceptibility to inhibition. Consequently, they explained these phenomena on the basis of a "frequency principle."

In the present experiments, the effect of pre-stimulus firing frequency on the reflex response differed from that predicted by Miles and Türker's "frequency principle." The excitatory reflexes were observed at a low BGA and the inhibitory responses were larger at a higher BGA than at a lower one. This difference between our and their result may be elicited from differences in experimental conditions and those in time course of the responses analyzed.

It is suggested from our result that when the BGA in a motor unit is lower, the motor-unit activity is increased reflexly to a fixed level. The reflex activity seems to be regulated such that it does not become too high. It is known, in fact, that the firing range in the final common path of the motor system is fixed and has an upper limit under natural conditions [18]. When the BGA in a motor unit is lower, an excitatory reflex is elicited and the firing frequency increases to a value that does not exceed the upper limit inherent in each motor unit. When the BGA in a motor unit is higher, an inhibitory reflex is elicited and the ongoing activity decreases or ceases. Such motor-unit activity, controlled so as not to increase too far, may reflect a protective reflex.

Jaw movement and reflex regulation of the masseter and temporal muscles. Because of the wide mandibular fossa in the rat, the sliding of the condyle in a rostrocaudal direction is possible over a long distance [19]. The mandible is
brought forward to bring the incisors into occlusion for ingestion, and the condyle is moved backward to bring molars into occlusion for mastication [3, 20]. Electromyographical data support the premise that the superficial masseter muscle is important in regulating the forward movement during the incisive stroke of ingestion and that the anterior temporal muscle functions most effectively during molar mastication [3].

The present study showed that the periodontal jaw reflexes depend on the site of a stimulated tooth within the dentition. Specifically, the susceptibility to excitation or inhibition in the masseter and temporal motor units varied according to the origin of the periodontal afferent information (Fig. 3). During incisal stimulation, the reversal level in the masseter motor unit was higher than that in the temporal motor unit. By contrast, during molar stimulation, the reversal level in the masseter motor unit was lower than that in the temporal moltor unit. The masseter and temporal motor units could easily be excited by incisal and molar stimulation, respectively, over a wide range of BGA.

The difference between the activities of the masseter and temporal muscles during ingestion by the incisors and mastication by the molars cannot be understood in terms only of a synergistic relationship between the muscles. In the present experiments, it became clear that the two muscles are reciprocally regulated in some cases. For example, the reciprocal reflex responses tended to be induced at an intermediate BGA in both the masseter and temporal motor units. When the magnitudes of the BGA in motor units of the two muscles were different, various reflex patterns, which depended on the BGA in each motor unit, were observed. It has been reported that a variation in reflex effects depends on the direction and intensity of the stimulus [10, 21]. However, in the present experiment, even when the direction and intensity of the stimulus were fixed, the reflex effects varied, depending on the BGA. The masseter and temporal muscles (represented by typical motor units) were regulated synergistically or reciprocally, depending upon the level of the BGA.

Inhibitory reflexes of the masseter and temporal muscles during incisal and molar stimulation. A motor unit's susceptibility to inhibition varied, depending not only on the BGA but also on the site of a stimulated tooth within the dentition. The inhibitory reflexes of the masseter and temporal motor units could easily be induced by molar and incisal stimulation, respectively, over a wide range of BGA.

Incisal stimulation produced greater inhibition in the masseter motor unit than did molar stimulation in the temporal motor unit. This difference may be related to the difference between muscle activity during a powerful stroke of phasic biting by incisors and that during molars' tonic grinding of food in the rat. The temporal muscle has been reported to exhibit continuous activity during molar chewing [22].

Histological studies of the superficial masseter and anterior temporal muscles show that the muscles consist mainly of phasic and tonic fibers, respectively [23]. Taking the results of the present study together with those of histological studies, we can conclude that the superficial masseter muscle, the activity of which is
enhanced mainly by incisors, and the anterior temporal muscle, which is activated mainly by molars, are particularly suitable for the phasic and tonic movements of the jaw, respectively.

**Spike amplitude of an individual motor unit and its reversal level.** In the present study, the thresholds for excitatory and inhibitory reflexes of the masseter and temporal muscles upon dental stimulation were lower in the smaller-amplitude and larger-amplitude motor units, respectively. The magnitudes of the excitatory and inhibitory reflexes of the jaw-closing muscles were larger in the smaller-amplitude and larger-amplitude motor units, respectively. These phenomena are in agreement with the "size principle" [24–26]. However, there are reports concerning motor units in which the results do not always follow the "size principle." The effects of cutaneous afferents on the motoneuron pool cannot be explained by the "size principle" [27–29]. Kanda et al. [28] reported that some low-threshold medial gastrocnemius motor units (smaller-amplitude units) exhibited a slowing of discharge or complete inhibition, and higher-threshold motor units (larger-amplitude units) were powerfully recruited by stimulation of the sural nerve in the cat.

In the present study, three typical combinations of reflex responses were obtained during simultaneous recordings from smaller-amplitude and larger-amplitude motor units (Fig. 6). These reflex responses followed the "size principle." However, not only the "size principle" but also the BGAs and the reversal levels of each motor unit must be considered in explaining these results.

When motor units of various amplitudes were active and their BGAs were almost equal, smaller-amplitude motor units tended to be excited and larger-amplitude units tended to be inhibited (Fig. 5). The reversal level was higher in smaller-amplitude motor units than in larger-amplitude ones. Figure 6C shows that the activity of the smaller-amplitude motor unit was inhibited because its BGA was higher than the reversal level, and the activity of the larger-amplitude one was excited because its BGA was lower than the reversal level.

The reversal level depended on the origin of periodontal afferent information and the amplitude of the motor units, and this relationship explains the variety in the reflex responses shown in Fig. 6. Inhibitory reflexes tended to be induced in larger-amplitude motor units of the temporal muscle during incisal stimulation. In such cases, inhibitory reflexes occurred even when the BGA in the motor unit was very low (Fig. 6B, 4 Hz). By contrast, the threshold for excitatory reflexes was the lowest and the magnitude of excitatory reflexes was the highest upon incisal stimulation of the smaller-amplitude motor units of the masseter muscle. The reversal level of each motor unit must be considered when we examine the susceptibility to excitation and inhibition of periodontal jaw reflexes in any motor unit. When the activity of a motor unit is lower or higher than the reversal level, the result is an excitatory or an inhibitory reflex, respectively.

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