The Physiology and Ontogeny of Daily Oral Behaviors

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Synopsis

In the masticatory system, activities of muscles are the main source of force. The daily activity of the jaw muscle is a measure of the total daily loading of the tissues involved. This article gives an overview on the recent assessments of the physiology and ontogeny of the daily use of the jaw muscles. Variations in the characteristics of daily activity could be linked to differences in the types of fibers composing the muscles as well as to the properties of the underlying bone, although these relationships are not absolute. Experimental decrease of the hardness of foods eaten by rats and rabbits showed a significant decrease in the number of daily bursts of feeding. These reductions in daily muscular activity were accompanied by higher mineralization of bone and by a transition toward “faster” fiber types in the muscles. It was revealed in rabbits that the characteristics of the daily activities of muscles (total duration of activity, number and lengths of bursts) were not altered during the transition from suckling to chewing and remained largely unaffected during further postnatal development. These results suggest that, despite large anatomical and functional changes, the average daily load on the jaw muscles by the masticatory system appears to be established before chewing develops and remains largely unchanged all the way through development. Whenever the daily muscular activity changes, this seems to have a significant effect on the properties of the tissues involved.

Introduction

This article assesses the physiology and ontogeny of the daily use of the jaw muscles as discussed at the symposium on the “Synthesis of Physiologic Data from the Mammalian Feeding Apparatus Using FEED, the Feeding Experiments End-User Database.” Data on the daily use of jaw muscles are available for only a limited number of species (rabbit, rat, and human) caused by the restrictions imposed by long-term electromyogram (EMG) recordings. The data on humans consists for the larger part of studies of sleep, including those examining bruxism. As these do not include the full range of daily oral behaviors but focus on a restricted number of behaviors, they are excluded from this selection which concentrates on the characteristics of the daily use of the jaw muscles, and their relationship with anatomical features of the muscles involved as well as those of the underlying bone.

Various studies have shown that the properties of muscle and bone are influenced by the loads imposed upon them. Artificial loading of muscle (e.g., nerve stimulation) and bone tissue (e.g., three-point bending) has shown that loading amplitude, loading number, and loading frequency are important factors in the adaptation of both tissues. The majority of the natural and spontaneous loadings are generated by muscles, and indirect evidence shows that these natural muscle forces are important for the adaptation of both tissues (Burr 1997; Turner 2000; Frost 2001).

Muscle function is usually examined for specific, and often rhythmic, tasks. However, each muscle is active during a large number of tasks, which require different amounts and levels of activity. For instance, except for specific tasks that involve often high and rhythmic activities, high levels of muscular activity are generated in an irregular fashion during fighting, while prolonged low activity is used to control
posture or respond to perturbations (Booth and Kirby 1992; Caiozzo et al. 1996; Edgerton and Roy 1996). The use of the muscles consists, therefore, of a wide range of different activities (Langenbach et al. 2004). It has also been shown that especially bone is receptive not only to individual high-amplitude loadings, but also for low-amplitude loadings at a high frequency (Qin et al. 1998).

To obtain knowledge about the relationship between the generated muscular forces and the architecture of muscle and bone, it is important to not concentrate on just one or a few behaviors, but to consider the entire range of behaviors of muscle. To accomplish that the muscle’s activity has to be recorded during at least a full day, so that all normal daily behaviors are included. This article reviews the work that has been performed recently in this area.

**Daily activity of jaw muscles—Recording technique and analysis**

Since the introduction of wire-electrodes (Basmajian and Stecko 1962), the regional activity of muscles can be recorded during a large variety of motor tasks. Because in these experiments, the subjects of study are connected by a cable to the recording unit, the recordings of normal behavior are restricted in time and space. Several techniques have been developed to minimize these limitations, but only radio-telemetry provided a true wireless solution. For example, Hensbergen and Kernell (1997) successfully used this technique to examine the daily activity of hind-limb muscles in the cat. In their study, the transmitters and batteries were worn in a jacket attached to a connector on the cat’s back, sending the data to a recording device. A comparable system has also been used in studies on humans and in which the use of muscles during sleep and bruxism, and the daily activities of jaw muscles were recorded (Miyamoto et al. 1996, 1999). In this case, the recorder and the unit for storage of data are placed in a portable device, thereby minimizing the limitations in body motion.

The first implantable device for transmitting the complex waveforms of muscular activity was utilized by Herzog et al. (1993). Its application, however, was limited because of its large size, a 10 cm-antenna that was not implanted, and a maximum transmitting time of 40 h. Since then, the technology has greatly progressed, but the method has sparsely been used to record muscle activities, probably due to the limited transmission range. Only recently have fully implantable systems, using radio-telemetry to transmit the biopotentials to a nearby PC, been available [e.g., Data Sciences International (DSI), St Paul, MN, USA], to examine the daily activity of muscles in freely moving animals. However, this system can only be used for caged animals as the range of transmission is limited. For the jaw muscles, this has been employed in the rabbit and rat.

The continuous collection of data lead to another problem: How to analyze the enormous amount of data (21.5 M datapoints/day/channel). Clearly, some data reduction executed in a semi-automatic way would come in handy. For this, the features of various commercially available software packages (e.g., Spike2, Cambridge Electronic Design Ltd., Cambridge, UK) can be used, expanded by custom-made subroutines. Hence, full-day recordings can be described by characteristics of activity such as the total duration of muscular activity (duty time) and the number and average length of bursts exceeding specified levels of peak activity. After exclusion of the largest 0.001% (i.e., 43 samples/day) EMG amplitudes, so as to eliminate possible artifacts, the peak activity was defined as the largest amplitude of the remaining 99.999% samples. The resulting duty times and the number of bursts are a good representation of daily muscular activity. It portrays the relative occurrence of both the most powerful activations (those exceeding 50%) and the differentiation in activations at lower levels. The noise level was always estimated. To ensure that no noise signal would be included, activations that fell within 10 times of the estimated noise level (in general, this was about two or three times the maximum detected noise) were excluded from the analysis.

Two remarks should be made about these long-term recordings. First, the recordings can be processed as normal EMG data, but the sampling frequency (250 Hz) is too low for a thorough analysis of frequencies. Second, the intramuscular bipolar electrodes register only a limited volume of the muscle. The jaw muscles consist of motor units confined at discrete regions (Herring et al. 1979; Weijs and Dantuma 1981; McMillan and Hannam 1991). Recordings could consequently be specific for only that region of the muscle. Indeed, various jaw muscles can be divided into several functionally distinct regions during tasks such as chewing and biting. In the following sections, these muscle regions will be specified when possible; unless stated differently, masseter stands for the superficial masseter muscle and temporal stands for the superficial temporal muscle. Generalizations of the results should be made with care.
Daily activity of jaw muscles—Variation of oral behaviors

In humans, long-term recordings, using surface electrodes, showed irregular activity periods of low activity of jaw muscles during sleep, while during the day generally longer and higher level activities were found. Almost all high-level activities of the masseter (895 ± 446) are associated with chewing. A much larger number of low-amplitude bursts (7081 ± 2664) could be found throughout the day (Miyamoto et al. 1996, 1999).

In the rabbit (Langenbach et al. 2004), continuous EMG recordings showed a vast variation in the activation of muscle, even in a 5-min period (Fig. 1A). Periods of feeding behavior (chewing and drinking) could simply be distinguished by their prolonged rhythmic character along with, for mastication (Fig. 1B), the highest levels of muscle activation. Most of the time, however, muscular activity was not present or was barely measurable and very irregular. Sessions of higher, but still irregular, muscle activation consisted of behaviors like grooming, walking around while exploring, etc. (Fig. 1C).

Fig. 1 Rectified muscular activity recording (EMG) of the rabbit superficial masseter, not representative for the total activity pattern during a full day. (A) Total of 5 min of recording, showing various behaviors. Boxes indicate the 20-s amplifications shown in B and C. (B) Mastication. (C) Some grooming behavior. Scale of the vertical axis is identical in all plots. Broken lines indicate 5 and 50% of peak activity (from Langenbach et al. 2004).

Animals masticated, on average, 27 min/day (range, 25–30 min), i.e., during ~2% of the time. Hourly calculations of duty times showed a clear circadian variation, indicative of animals using their jaw muscles less during the early daylight hours (rabbit; Langenbach et al. 2004), or the entire daylight period (rat; Kawai et al. 2007).

Daily activity of jaw muscles—Variations among muscles

Comparable differences among muscles were found for number of bursts and duty time in the rabbit (van Wessel et al. 2005b) and the rat (Kawai et al. 2007). In the rabbit, for muscle activations exceeding the 5% level, the temporalis showed significantly (P < 0.05) more bursts (around 205,000/day) than did the superficial and deep masseter (both about 90,000/day). The digastric (about 120,000/day) and medial pterygoid (about 115,000/day) did not show significant differences in the number of bursts. For muscle activations exceeding the 5% level the duty time of the temporalis was significantly (P < 0.05)
higher than that of the other muscles, except for the digastric. In the rat, the digastric showed many more bursts (125,000/day) than did the masseter muscle (55,000/day).

As the activity level increased, a clear decrease was seen in number of bursts and in duty time. For muscle activations exceeding the 20% level, the number of contractions was limited to about 50,000/day, occupying about 45 min of the entire day. At this level, no significant differences either in number of bursts or in duty times were detected among muscles. However, for activations exceeding the 50% level, the superficial masseter and medial pterygoid showed significantly ($P<0.05$) higher numbers of bursts and longer duty times than did the other jaw muscles. The differences in numbers of bursts among muscles were reflected by the differences in duty time. In contrast, mean duration of burst was similar for all muscles. This indicates that differences in duty time among muscles are mainly determined by variation in number of bursts and not by changes in duration of bursts.

In the rat, the digastric muscle remained the most active muscle for activities exceeding the 20% level. Only for activities exceeding 80%, did the digastrics show a significantly lower number of bursts compared to the masseter (respectively, 114 and 160 bursts/day).

The number of bursts registered in the rat and rabbit exceeds by far the number of bursts revealed in humans. This is caused by the type of electrodes used. Intramuscular wire electrodes are able to record muscular activities with much lower amplitudes than do surface electrodes, as used in studies of humans. So, the numbers reported in the studies on humans are analogous to the number of bursts at higher activity levels in rat and rabbit.

**Daily activity of jaw muscles—Relation to the composition of fiber types**

In the rabbit, a positive intermuscular correlation between duty time and the number of slow-type fibers ($R=0.90$, $P<0.05$) was found for muscle activations exceeding the 20% level (van Wessel et al. 2005c). This positive correlation became stronger for activations exceeding higher levels (Table 1, $R>0.94$, $P<0.05$). Similarly, for the number of bursts per day, the positive correlation with the number of slow-type fibers became significant for activations exceeding the 30% level ($R=0.96$, $P<0.01$) and remained significantly positive for higher level activations ($R>0.95$, $P<0.01$). Analysis of the cross-sectional areas revealed that for activations exceeding the 30% and higher levels (except for 90%), the correlation between the cross-sectional area of the slow-type fibers and the duty time was significantly positive ($R>0.89$, $P<0.05$). Hence, muscles that were activated more intensely contained a higher percentage of relatively thick slow-type fibers. In the jaw muscles, it seems that the commonly known “size principle” (Henneman 1965) applies only for high-level activation (>$20\%$). Other recruitment strategies have been proposed; for instance, recruitment depending on mechanical suitability (Hannam and McMillan 1994; van Eijden and Turkawski 2001). The latter one might be effective during the low-level activations.

Among the jaw muscles of the rat, the digastric contains the highest amount of slow-type fibers combined with the highest duty time for activities exceeding the 5% level. Also, intermuscular variations indicate a significant positive relationship ($P<0.05$) between the percentage of IIX fibers and muscle activities exceeding the 50% level (Kawai et al. 2009). This suggests that this fatigable type of fiber is crucial for generation of the greater muscle forces.

### Table 1

<table>
<thead>
<tr>
<th>Slow-type fibers (%)</th>
<th>Cross-sectional area slow-type fibers</th>
<th>Duty time</th>
<th>Number of bursts</th>
<th>Duty time</th>
<th>Number of bursts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Activity level (%)</td>
<td></td>
<td>0.02</td>
<td>0.11</td>
<td>0.56</td>
<td>0.60</td>
</tr>
<tr>
<td>20</td>
<td></td>
<td>0.90*</td>
<td>0.74</td>
<td>0.76</td>
<td>0.51</td>
</tr>
<tr>
<td>50</td>
<td></td>
<td>0.94*</td>
<td>0.97**</td>
<td>0.91*</td>
<td>0.85</td>
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<tr>
<td>90</td>
<td></td>
<td>0.94*</td>
<td>0.95**</td>
<td>0.58</td>
<td>0.70</td>
</tr>
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</table>

*a* Intermuscular correlation coefficients (i.e., $R$) of the relationship between percentage of slow-type fibers and cross-sectional area slow-type fibers (from van Wessel et al. 2005c).

*b* Intermuscular correlation coefficients of the fiber’s cross-sectional area in relation to the duty time or the number of bursts are also shown for these four levels (B).

$*P<0.05$, **$P<0.01$. 

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![Image](https://academic.oup.com/icb/article-abstract/51/2/289/922901/attachment1/12829011)
In the literature, it is acknowledged that muscles containing a high fraction of slow-type fibers are more active during the day than those largely composed of fast-type fibers (Monster et al. 1978; Kernell and Hensbergen 1998). This differentiation is related to the orderly recruitment of motor units based on the size principle (Henneman 1965; Hennig and Lømo 1985). According to this principle, the smaller slow-type motor units are recruited first, at low levels of intensity, while the larger (and often fast-type) units join in at higher levels of intensity. The positive correlation between the amount of activation exceeding the 20% level and the percentage of slow-type fibers suggests that in the jaw muscles, the principle of orderly recruitment of motor units applies to high-level activation (>20% peak activity), but not to low-level activation (<20%). Other recruitment strategies have been proposed (Wakeling and Rozitis 2005); for instance, motor-unit recruitment depending on mechanical suitability. Such recruitment has been reported especially for the jaw muscles (Hannam and McMillan 1994; van Eijden and Turkawski 2001). The above-mentioned results suggest that different recruitment strategies exist between powerful and nonpowerful motor tasks, and possibly among different species.

Mechanical properties of food influence the activity of the jaw muscles. In rabbits, fed with a 12-fold softer food, the daily number of bursts and the duty time of the masseter were lowered by about 30% but only for activities of a low intensity and only during the first weeks after the diet change (Grünheid et al. 2010). The activity characteristics of other jaw muscles were unaffected. This reduction in activity was accompanied by changes in the phenotypic properties of masseter muscle fibres assessed 12 weeks after the diet change (Kawai et al. 2010). According to this principle, the smaller slow-type motor units are recruited first, at low levels of intensity, while the larger (and often fast-type) units join in at higher levels of intensity. The positive correlation between the amount of activation exceeding the 20% level and the percentage of slow-type fibers suggests that in the jaw muscles, the principle of orderly recruitment of motor units applies to high-level activation (>20% peak activity), but not to low-level activation (<20%). Other recruitment strategies have been proposed (Wakeling and Rozitis 2005); for instance, motor-unit recruitment depending on mechanical suitability. Such recruitment has been reported especially for the jaw muscles (Hannam and McMillan 1994; van Eijden and Turkawski 2001). The above-mentioned results suggest that different recruitment strategies exist between powerful and nonpowerful motor tasks, and possibly among different species.

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In a comparable experiment (using a powder as food) performed on rats, similar results were found. In this case, also the masseter showed a lower number of activity bursts in reaction to the lowered hardness of food. The rat’s masseter does not contain slow-type fibers, but within the collection of fast-type fibers an increase in the fastest types (IIx and IIB) was observed (Kawai et al. 2010). Except for these modifications of the masseter, there was also an increase in the daily activity of the digastric in animals fed a softer food. This increase in daily activity was not accompanied by any change in the fiber-type composition.

In both animal models, the reduction in dietary consistency induced changes in the MyHC composition and fibre cross-sectional area of the masseter muscle, but not in other jaw closers. During chewing, less muscle force is required to break soft food than to break hard food. The temporalis is often active during the early jaw-opening stages, and less involved in the generation of occlusal forces. The masseter muscle elevates the mandible and generates occlusal force during the power stroke (Widmer et al. 2003). It appears that the reduction in dietary consistency altered only the functional loading of the muscles that generate the force necessary to crush the pellets. The increase in daily digastric activity (in the rat) might be the result of a different method of feeding. Powdered food was mainly licked and not processed in a chewing fashion. The reduction in the number of muscle contractions was accompanied by a transition toward a greater proportion of faster fiber types. It is known that disuse of muscles leads to fast-fiber types (d’Albis et al. 1995; Oishi et al. 1998).

**Daily activity of jaw muscles—Relation to bone architecture**

The anterior region of the rat mandible shows a higher degree of mineralization (1194 ± 17 mg hydroxyapatite/cm³) than does the ramus region (986 ± 22 mg hydroxyapatite/cm³) (Tanaka et al. 2007). This is confirmed by comparable data from the pig (Mulder et al. 2006) and preliminary data from the rabbit. The area of elevated mineralization correlates with the locations of attachment of the jaw muscles, mainly on the mandibular ramus. Their activity possibly contributes to a larger number of stimuli for turnover of bone in the posterior area of the mandible. Increased turnover of bone results in relatively more new bone tissue, which is little mineralized so that the average degree of mineralization becomes lower. In the rabbit, the degree of mineralization of individual muscle-attachment sites was related to the characteristics of daily activity. Preliminary data show that interindividual variations in mineralization were negatively related to the number of daily bursts of activity of the masseter that exceeded the 50% level (Fig. 2). Thus, the attachment sites of highly active muscles is less mineralized than those of less active muscles. No such relationship was found for the temporalis and digastric muscles. This can be explained by the fact that,
because of differences in muscle-sizes in the rabbit, the amplitude of the muscle forces for the masseter are higher than for other jaw muscles.

Tanaka et al. (2007) fed rats a soft diet while they were kept in a gnaw-free cage. Compared to rats on a normal diet, the posterior and anterior regions of the mandible showed a higher degree of mineralization (respectively, +31 and +47 mg hydroxyapatite/cm^3) than did the animals on a soft diet (P<0.05). As these animals had to produce lower occlusal forces, their jaw muscles possibly were less active. On a daily basis, their muscles generated fewer stimuli to the bone, resulting in a lower bone turnover and a higher degree of mineralization.

**Daily activity of jaw muscles—Ontogeny**

During development, the anatomy of the jaw system alters. Due to the vertical growth of the face, the mandibular ramus increases its height and the muscles acquire different action lines. The primary dentition is simultaneously exchanged for a permanent one. These substantial anatomical changes affect the biomechanics of the system and bring about different motion boundaries of the mandible. It is feasible that along with these large anatomical changes, the daily use of the jaw muscles shows variation.

Miyamoto et al. (1996, 1999) used surface electrodes to examine the daily use of the masseter in children and adults. Comparison of the number of bursts between children and adults revealed that children produced significantly more daily bursts of activity (approximately 3000) than did adults (approximately 2100). This difference was the result of a higher number of low-level activities during the day and greater time devoted to sleep in the children (P<0.01). The number of bursts during meal time was comparable.

In the rabbit, the duty time and number and duration of bursts (van Wessel 2005a, 2005b, 2005d, 2006) do not change during maturation. This is remarkable, since maturation of the jaw muscles is characterized by large anatomical changes, such as an increase in fiber length and in cross-sectional area of the muscle (Weijs et al. 1987), as well as in substantial changes in fiber-type composition (Bredman et al. 1992; Eason et al. 2000; English and Schwartz 2002). Despite these morphological changes, the mastication pattern of young animals resembles that of adults (Weijs et al. 1989; Langenbach et al. 1992). The pattern of contraction and daily use are established before the morphological changes have been completed.

Although the overall characteristics of daily activity did not change during maturation, analysis of the interindividual variation (expressed by the COV) of the duty times and numbers of bursts revealed that for levels of activation exceeding 2 and 5% (van Wessel 2005b, 2005c), all jaw muscles, except the medial pterygoid, showed a significant (P<0.05) decrease in these characteristics during development. This decrease in interindividual variation could be related to a drop in neuromuscular plasticity (Kernell 1998) and alterations in afferent feedback mechanisms (Westerga and Gramsbergen 1993) during maturation.
Conclusions
Except for the well-described muscle activities during chewing and other feeding-related behaviors, the muscles in the jaw system produce large numbers of activity bursts, in the rabbit about, or even exceeding, 100,000 bursts. As everyday consists of 86,400 s, the jaw muscles generate more than one burst every second. Most of these bursts are of low-amplitude. Despite large anatomical and functional changes, the daily muscular loading remains largely unchanged during development in rabbits. In humans, there is a clear decrease in the number of bursts.

Focusing on the high-amplitude bursts, the masseter and medial pterygoid are the most active muscles. Variation among muscles and individuals are represented by associated differences in fiber-type composition and in degree of mineralization of the attachment sites. Muscles with a higher number of bursts have a greater number of slow-type fibers, and less mineralized attachment sites. When the number of activities was experimentally lowered, there was a decrease of the proportion of slower fiber types, and an increase in the degree of mineralization of the bone. The data suggest that the daily amount of muscle loading optimizes the function of the jaw system by adaptation of the tissues involved.

References