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Burst characteristics of daily jaw muscle activity in juvenile rabbits

T. van Wessel[1,*], G. E. J. Langenbach[1], N. Kawai[2], P. Brugman[1], E. Tanaka[2] and T. M. G. J. van Eijden[1]

[1]*Department of Functional Anatomy, Academic Centre for Dentistry Amsterdam (ACTA), Universiteit van Amsterdam and Vrije Universiteit, Meibergdreef 15, 1105 AZ, Amsterdam, The Netherlands* and [2]*Department of Orthodontics and Craniofacial Developmental Biology, Hiroshima University Graduate School of Biomedical Sciences, 1-2-3 Kasumi, Minami-ku, Hiroshima 734-8553, Japan*

*Author for correspondence (e-mail: t.vanwessel@amc.uva.nl)

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Summary

Muscle activation varies with different behaviors and can be quantified by the level and duration of activity bursts. Jaw muscles undergo large anatomical changes during maturation, which are presumably associated with changes in daily muscle function. Our aim was to examine the daily burst number, burst length distribution and duty time (fraction of the day during which a muscle was active) of the jaw muscles of juvenile male rabbits (*Oryctolagus cuniculus*). A radio-telemetric device was implanted to record muscle activity continuously from the digastric, superficial and deep masseter, medial pterygoid and temporalis during maturation week 9–14. Daily burst characteristics and duty times were determined for activations, including both powerful and non-powerful motor behavior. All muscles showed constant burst numbers, mean burst lengths and duty times during the recording period. Including all behavior, the temporalis showed significantly larger daily burst numbers (205 000) and duty times (18.2%) than the superficial and deep masseter (90 000; 7.5%). Burst numbers and duty times were similar for the digastric (120 000; 11.1%) and medial pterygoid (115 000; 10.4%). The temporalis and deep masseter showed many short low activity bursts (0.05 s), the digastric showed many long bursts (0.09 s). For activations during powerful behaviors the superficial masseter and medial pterygoid had the largest burst numbers and duty times. Both muscles showed similar burst characteristics for all activation levels. It was concluded that activation of the jaw muscles is differently controlled during powerful and non-powerful motor behaviors and the functional organization of motor control patterns does not vary from 9 to 14 weeks of age.

Key words: EMG, duty time, motor control, burst number, burst length, rabbit, *Oryctolagus cuniculus*.

Introduction

Most muscles can be used to perform different types of motor behavior that range between short powerful contractions for the generation of rapid movements and prolonged low level contractions for the maintenance of posture. These different types of motor behavior are reflected in the muscle's electromyogram (EMG) and can be quantified in terms of the level and duration of EMG bursts. The total duration of muscle activity during the day, which is defined by the duty time (Hensbergen and Kernell, 1997; Langenbach et al., 2004), is associated with both the number of bursts and their lengths generated during the different motor tasks. Differences in duty time between muscles have been related to their fiber type composition (Monster, 1978; Kernell and Hensbergen, 1998). Muscles largely involved in postural activities generally show high duty times and contain a large percentage of slow type fibers. In contrast, more phasically active muscles show relatively low duty times and generally contain a small percentage of slow type fibers.

A few studies have determined the duty time over longer time periods, including a wide range of daily behaviors (hindlimb muscles in cat, Hensbergen and Kernell, 1997; monkey, Hodgson et al., 2001; jaw muscles in human, Miyamoto et al., 1996, 1999; rabbit, Langenbach et al., 2004; van Wessel et al., 2005). Although duty time is a valuable parameter, it is only a general indicator of muscle use and cannot distinguish between different types of activation, such as phasic or tonic. Further differentiation of the duty time into the number and duration of the EMG bursts at various activity levels could provide additional information on normal daily muscle use and motor control mechanisms.

Jaw muscles participate in a wide range of oral behaviors, during which timing and coordination between the muscles differ (Langenbach et al., 1992; Blanksma et al., 1995, 1997). These variations in muscle use can be related to differences in duty time between the muscles (Langenbach et al., 2004; van Wessel et al., 2005). The latter study found that duty times of

the jaw muscles do not change during juvenile maturation. This is remarkable since maturation is characterized by large anatomical and functional changes in these muscles (Weijs et al., 1987; Bredman et al., 1990, 1992; Langenbach et al., 1992; English et al., 1998, 2002), and a general increase in efficiency in timing and coordination of all musculoskeletal systems (Westerga and Gramsbergen, 1993; Muir, 2000). Although these changes are not reflected by a modification of the duty time during the juvenile period, the activity profile of the different muscles might differ in the number and/or duration of the EMG bursts.

We therefore examined the daily burst number, burst length and duty time of the jaw muscles in juvenile rabbits. Radio-telemetry-enabled wireless EMG recording was as natural a measure for muscle behavior as possible. The duty time has been shown to differ between jaw muscles (van Wessel et al., 2005). As the jaw muscles are diverse in their function and activated in different combinations with varying duration, this duty time obtained by van Wessel et al. (2005) was used in the present study and extended by differentiation into number and length of the activity bursts. It was hypothesized that the muscles differ from each other in daily burst number and burst length. Furthermore, the large maturational changes in anatomy and function were expected to be related to a modification in the number and/or length of the bursts over time.

Materials and methods

Telemetric system

The telemetric system [Data Sciences International (DSI), St Paul, MN, USA] used in this study has been described previously (Langenbach et al., 2002, 2004; van Wessel et al., 2005). In brief, small implants (45 mm×17 mm×10 mm, 14 g; 3 or 4 channels) were used to record muscle activities. Muscle potentials were registered by stainless steel wire electrodes, filtered in the implant (first order low-pass filter, 158 Hz) and sampled (250 Hz) for 6 weeks continuously (i.e. 21 600 000 samples/channel/day). The sampled potentials were transmitted to two receivers and stored onto a PC hard disk for analysis. Despite the low sampling frequency, the sampled potentials are a good representation of the original biopotentials (Langenbach et al., 2002).

Surgical implantation and recording procedure

The surgical procedure was essentially the same as described previously (van Wessel et al., 2005). Under general anesthesia, nine juvenile male New Zealand White rabbits *Oryctolagus cuniculus* L.; age, 8 weeks; mass range, 1200–1800 g) were provided with a telemetric implant. The animals showed no visible muscular or skeletal abnormalities and had adult dentition from the start of the experiment (age 8 weeks). The implant was subcutaneously fixed in the shoulder area of the animal. The bipolar electrodes (diameter 0.45 mm) were inserted, parallel to the fiber direction, into the right jaw muscles. The electrodes were fixed at the muscle surface. The distance between the electrodes was 1–3 mm and the effective electrode length was 7 mm. In different combinations three or four jaw muscles were simultaneously recorded from each animal (Fig. 1A).

Each animal was held in a standard cage (100 cm×55 cm×45 cm) and provided with *ad libitum* pellets, hay and water and, except for the daily care, left undisturbed to minimize any external influence. Day-night rhythm was ensured by automatic dimmed lighting (07:00 h–19:00 h). All animals were weighed twice a week to monitor growth. The experiment was approved by the Animals Ethics Committee of the Medical School of the University of Amsterdam.

Recording of muscle activities started 2–3 days after surgery when the animal had regained common feeding behavior. The daily behavior of four animals was monitored by video surveillance (infra-red CCD camera, VCB-3372P; resolution: 560×400 TV lines; video frame rate: 15 frames s^{-1}; Sanyo Electric Co. Ltd, Osaka, Japan). Following the 6-week recording period (maturation weeks 9–14), the animals were sedated (Hypnorm, Janssen Pharmaceutica, Tilburg, The Netherlands) and killed by an overdose of pentobarbital (Nembutal, Sanofi Sante, Maassluis, The Netherlands), after which signals were recorded for another 5 min to determine the level of recorded noise. The electrode locations were verified by dissection.

Analysis

Muscle activity was quantified per 24 h period. Two days were analyzed for each maturational week, except for week 14, when only 1 day was analyzed. The recordings were filtered to remove motion-artifacts (5 Hz high-pass), rectified and averaged [20 ms window, 5 samples; Spike2 v5.0, Cambridge Electronic Design (CED), Cambridge, UK]. Total signal loss due to transmission problems was generally less than 5% of the total time and usually occurred during exploring behavior when the animal with transmitter moved near to the limits of the volume of reception. With one animal there were exceptionally large dropout periods, up to 165 min per day.

Per day and for each muscle, the amplitude of all processed samples was determined (resolution 1 μV). Based on the distribution of amplitudes of each muscle over the different days, 0.001% (i.e. 43) of the samples with the largest amplitude were excluded from the analysis to eliminate possible artifacts. The largest amplitude of the remaining 99.999% of the samples indicated the maximum muscle activity for that day and was defined as the peak-EMG. Muscle activity level was expressed as a percentage of this peak-EMG.

Duty time was defined per 24 h period as the fraction of this period that a muscle was active. The duty time was determined for muscle activities exceeding 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80% and 90% of the peak-EMG. For example, the duty time for activities exceeding 5% peak-EMG is the total relative duration of all EMG samples having amplitudes larger than 5% of the peak-EMG of that day.

To quantify burst number and length in relation to activity level, a custom-made code for the Spike2 software was used. The rectified and averaged recordings (Fig. 1B) were scanned

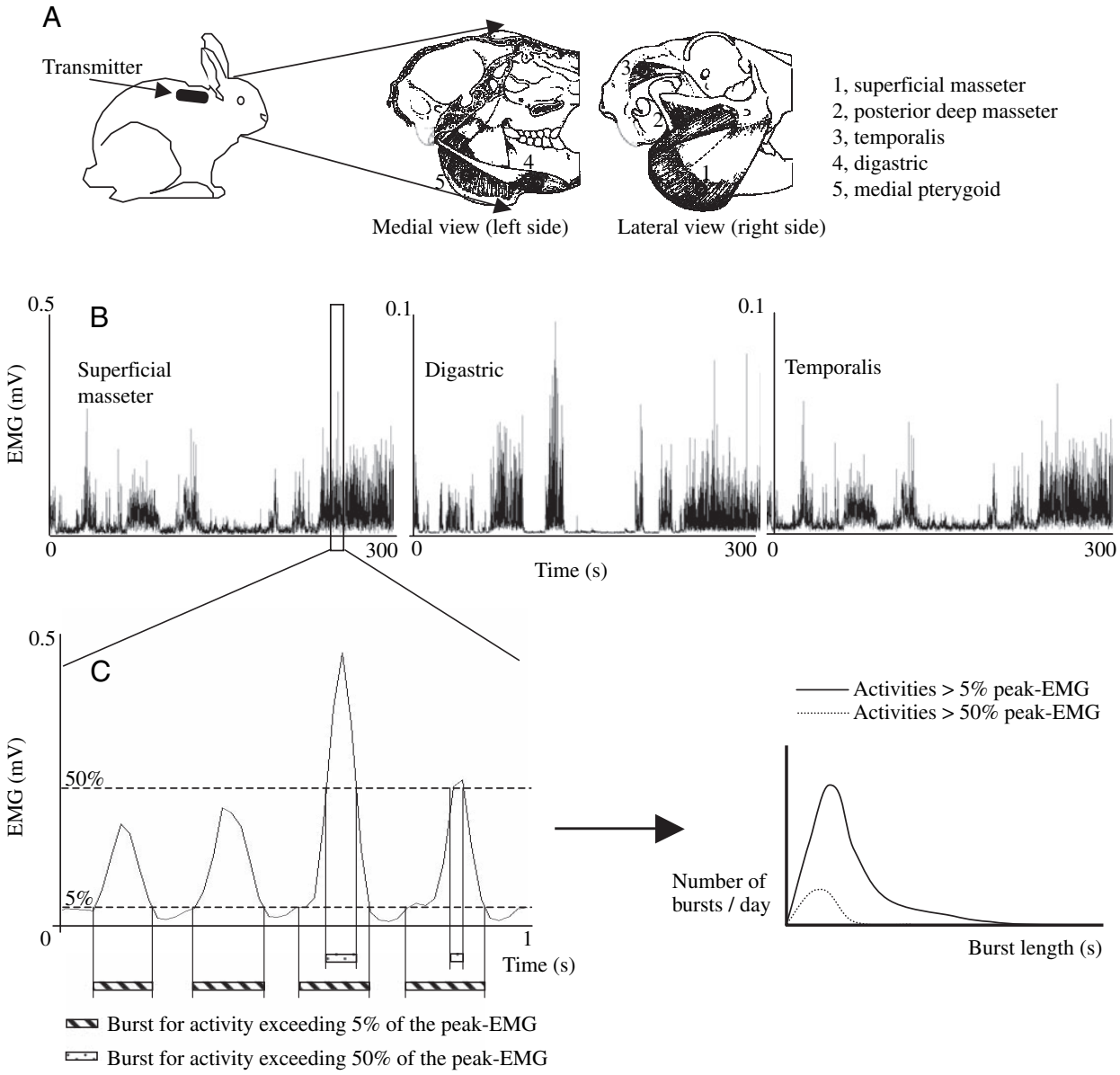

Fig. 1. Electrode locations and method of data analysis. (A) Implantation site of the transmitter in the neck area and locations of the electrodes in the five jaw muscles. (B) Examples of 5 min of simultaneously recorded EMG of three jaw muscles. (C) The enlargement (left) shows 1 s of muscle activity from the superficial masseter. The broken lines indicate the levels 5% and 50% of the peak-EMG. A burst was classified as a series of consecutive samples exceeding a predefined level of activity. The total number of bursts during 1 day was classified for muscle activities exceeding the 5% and 50% levels, which resulted in the distributions of burst number as a function of burst length (right). Note that the 5 min example (B) is not representative of the depicted distributions in C.

to locate all the bursts exceeding the above-mentioned activity levels. A burst was defined as a series of consecutive samples exceeding a predefined level of activity (Fig. 1C, left). For the various levels all bursts were indexed for their length (20 ms resolution). The total burst number, mean burst length (± S.D.), median burst length and distribution of burst number as a function of burst length (Fig. 1C, right) were determined for each muscle and the various activity levels.

Data exclusion

On three occasions the electrode pair dislodged before the end of the experiment, therefore these muscles were excluded from the analysis. Eventually, 27 muscles were processed in the analysis, i.e. digastric (N=5), superficial masseter (N=5), posterior deep masseter (N=6), medial pterygoid (N=6), and temporalis (N=5). For each muscle the level of noise $[(\Sigma y^2 N^{-1})^{0.5}$, where y = sample amplitude and N = number of samples] and the maximum noise amplitude (2–9 μV) were estimated. In general, the estimated noise levels were below the 1% peak-EMG. However, in some of the recorded muscles the maximum noise amplitude approached the 5% peak-EMG. Therefore, the 5% activity level was taken as the lowest level

in which, for all recorded muscles, noise was not included in the analyzed signals.

Statistics

Over all animals, means and S.D. values of the daily duty times, number of bursts, individual mean burst length, and median burst length were calculated for each muscle, and for all examined activity levels. For each muscle and for each activity level separately, a general linear model (repeated measures) was used to test whether maturation had an effect on normally distributed averages of burst number, mean and median burst length or duty time. Parametric testing was used to reveal interaction effects between activity level and maturation. In cases that did not meet the criteria for homogeneity of variance the Greenhouse–Geisser correction was applied to calculate the adequate *P*-value. Differences between muscles in burst number, mean and median burst length or duty time were tested using independent *t*-tests on normally distributed averages, for each activity level and each analyzed day. In each animal a different combination of muscles was continuously recorded. Therefore, independent testing was used to reveal differences between muscles. Changes in peak-EMG during maturation were also tested for each muscle separately using a general linear model (repeated measures). For each muscle and for all analyzed days the interindividual variation in burst number and burst length was expressed by the coefficient of variation [COV=(S.D./mean)×100%]. Changes during maturation in the interindividual variation for daily burst number and burst length were tested using one-way analysis of variance (ANOVA) on the COVs of these parameters for activations exceeding the 5%, 20%, 50% and 90% levels. In all tests a *P*-value of less than 0.05 was considered statistically significant. Statistical tests were performed using SPSS statistical software package (SPSS Inc., Chicago, IL, USA), version 11.5.1.

Results

All animals continued to grow throughout the recording period, resulting in a doubling of the weight of each animal. Video recordings clarified that during the first post-surgical days only the animals showed some modified behavior, such as less locomotion and decreased food intake, together with some reduced defecation; however, water intake remained normal.

The continuous EMG recordings showed a wide range of muscle activities (Fig. 1B). The peak-EMG varied among muscles and individuals (range for the different muscles: digastric, 0.07–0.62 mV; superficial masseter, 0.21–0.63 mV; deep masseter, 0.06–0.87 mV; medial pterygoid, 0.14–1.22 mV; temporalis 0.05–0.75 mV). During maturation the averaged peak-EMG values showed no significant differences for the individual muscles except for the superficial masseter, which showed a significant (d.f.=10, P=0.03) increase in peak-EMG from week 9–11. During maturation no statistically significant changes were detected in any of the muscles for burst number (d.f.=10, P>0.1), mean burst length (d.f.=10, P>0.2) or duty time (d.f.=10, P>0.2) for any of the tested activity levels. No interaction effects were found between maturation and activity level. Including almost all muscle activities (i.e. exceeding 5% peak activity), around 205 000 bursts per day were registered (temporalis, week 14), occupying one fifth of the total time (Fig. 2A). For the most powerful activities only (i.e. exceeding 90% peak activity), the number of bursts for any of the muscles was limited to a maximum of 120 each day, occupying only a few seconds (0.003% of the total time).

The mean burst length did not differ between the muscles for any of the tested levels (Fig. 2B). In contrast, significant differences between muscles were found for burst number and duty time (Fig. 2A,C). For muscle activities exceeding the 5% level, the temporalis showed significantly (d.f.=6, P<0.05) more bursts (around 205 000 per day in week 14) than the superficial and deep masseter (both around 90 000 per day in week 14) (Fig. 2A). The digastric (around 120 000 per day in week 14) and medial pterygoid (around 115 000 per day in week 14) did not show significant differences in burst number. For muscle activities exceeding the 5% level the duty time of the temporalis in week 14 was significantly (d.f.=6, P<0.05) higher than that of the other muscles, except for the digastric (Fig. 2C).

As the activity level increased a clear decrease was seen in burst number, mean burst length and duty time. For muscle activities exceeding the 20% level the number of contractions was limited to about 50 000 per day in week 14, occupying only 3% of the total time (i.e. about 43 min). At this level no significant differences in burst numbers and duty times were detected between the muscles. However, for activities exceeding the 50%, 60%, 70%, 80% and 90% levels the superficial masseter and medial pterygoid showed significantly (d.f.=6, P<0.05) larger burst numbers and duty times than the other three muscles (Fig. 2).

The distribution of burst lengths (Fig. 3) showed that for activities exceeding the 5% level the temporalis and deep masseter produced many short bursts. This was reflected in a median burst length of 0.03 s for both muscles, which differed significantly (d.f.=6, P<0.05) from the median burst length (0.05 s) of the digastric, superficial masseter and medial pterygoid. For the temporalis and deep masseter, large numbers of bursts (19% of the total) were found at a burst length of 0.05 s (Fig. 3). In contrast, the digastric showed a large number of bursts (16% of the total) at a longer burst length of 0.09 s, whereas the superficial masseter and medial pterygoid showed a bimodal distribution with a large numbers at burst lengths of 0.05 s (13% of the total) and 0.11 s (16% of the total). For contractions longer than 1.0 s the temporalis showed a large amount of bursts compared to the other muscles. For example, the 18% duty time of the temporalis in week 14 contained 1.5% duty time of these bursts longer than 1.0 s.

As the activity level increased the bimodal pattern of the distribution curves for the superficial masseter and medial

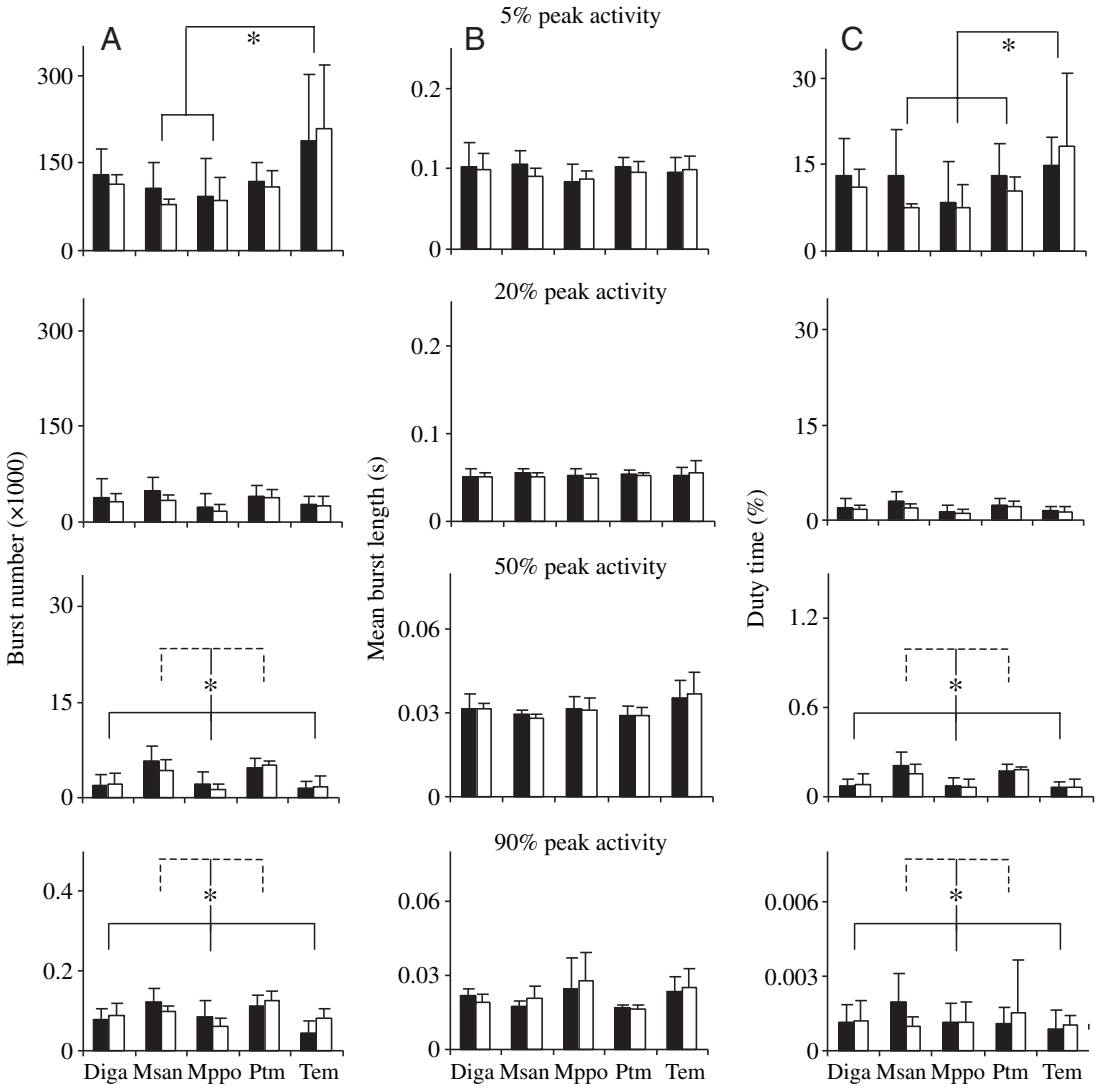

Fig. 2. (A) Burst number, (B) mean burst length (s) and (C) duty time (%) for 1 day in week 9 (filled bars) and week 14 (open bars). Muscle activities exceeding 5%, 20%, 50% and 90% of the peak-EMG for all tested muscles are shown. Values are means ± S.D. Diga, digastric; Msan, superficial masseter; Mppo, posterior deep masseter; Ptm, medial pterygoid; Tem, temporalis. Asterisks indicate significant differences (P<0.05). Asterisks in A and C exceeding 50% and 90% indicate that the superficial masseter and medial pterygoid significantly differed from the digastric, deep masseter and temporalis.

pterygoid disappeared and the largest burst numbers gradually shifted to shorter burst lengths similar for all muscles. For activities exceeding the 20% level the distribution curves of the digastric, superficial masseter and medial pterygoid were higher compared to those of the temporalis and deep masseter. For activities exceeding the 50% level the distribution curves of the superficial masseter and medial pterygoid were higher compared to the other three muscles. These visually detected differences between the burst length distributions were supported by statistically evaluated mean and median values of these distributions. Although the distributions of the muscles look somewhat different between week 9 and week 14, no significant differences were detected in burst number, mean and median burst length and duty time during maturation.

Discussion

In this study radio-telemetry was used to record daily activity of the jaw muscles during a 6-week recording period. The analysis method used the peak-EMG of each muscle as a reference to determine the duty times, burst numbers and burst lengths. Exclusion of the 0.001% (i.e. 43) samples with the largest amplitude resulted in the most consistent peak-EMG over the entire recording period in all animals. By using this peak-EMG as a reference for all examined activity levels, possible artifacts were excluded. The peak-EMG differed between muscles, which suggests a difference in the number of activated fibers in the pick-up area of the electrodes. It is unknown to what extent the peak-EMG and the relative EMG can be functionally compared between muscles. However, previous studies (Langenbach et al., 2002, 2004; van Wessel et

al., 2005) have shown that peak-EMG was stable for a prolonged period and that the resulting duty times are a reliable reflection of the bio-potentials and the daily recurrence of oral behavior. Movement artifacts related to the 3–4 Hz rhythmic pattern during several behaviors were eliminated by the 5 Hz high pass filter, whereas cross-talk from other muscles was minimized by the bipolar electrode configuration. The limited frequency range and low sampling frequency of the system do not allow reliable frequency analysis of the recorded signals.

Although this paper discusses differences between muscles and individuals during development it should be noted that the activity of only a small muscle region was recorded. In this paper we have focused on cumulative data, showing the amount of muscle activity exceeding predefined levels, as this serves as a measure for the complete daily loading under which a muscle functions. Further analysis of video recordings could clarify the relationship between specific behavior and muscle activation exceeding different levels. The duty time has

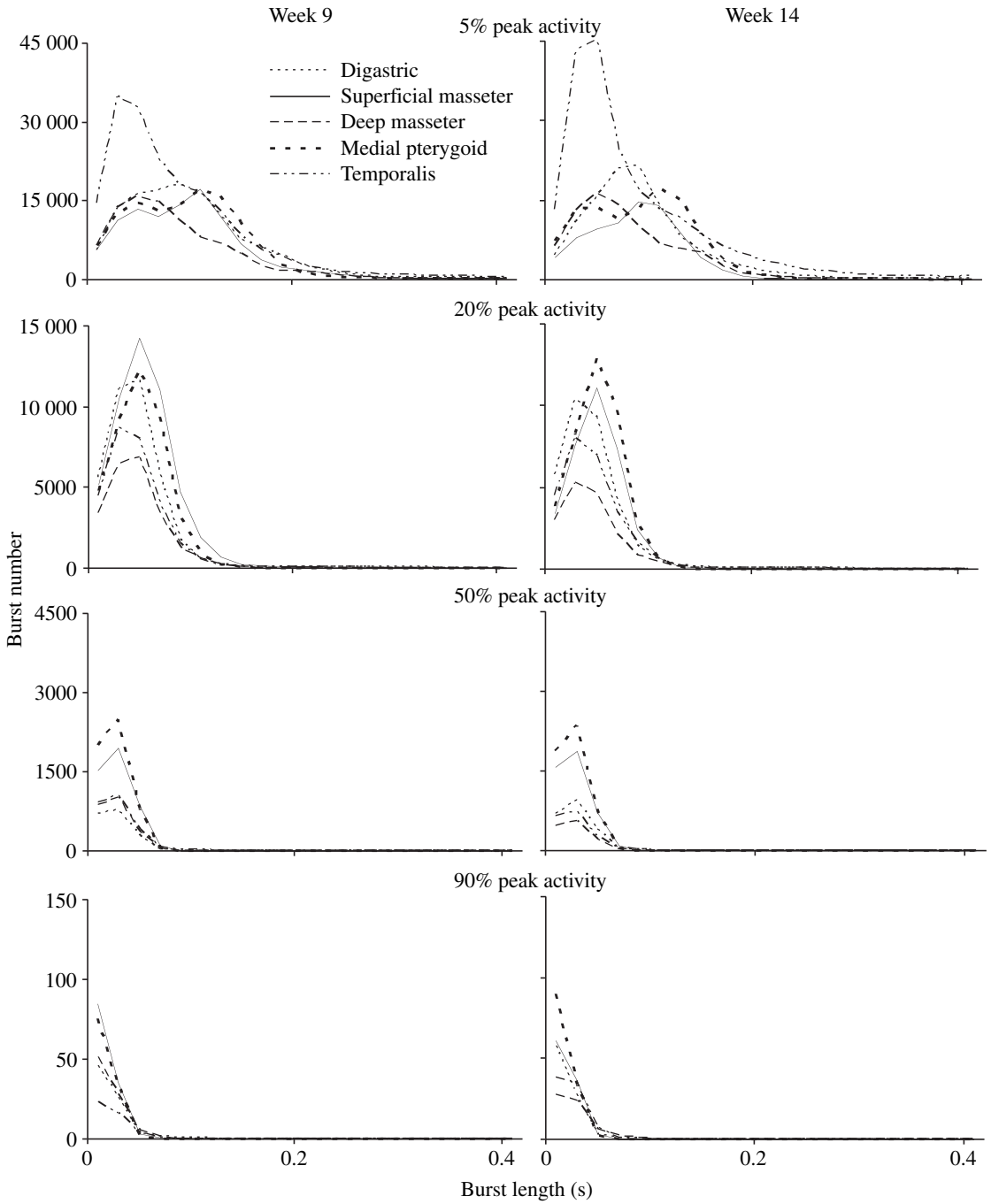

Fig. 3. Distributions of burst lengths of five jaw muscles averaged for all animals. Distributions show burst number as function of burst length for 1 day in week 9 (left) and week 14 (right) for muscle activities exceeding 5%, 20%, 50% and 90% of the peak-EMG. For clarity, only bursts up to 0.4 s are shown.

previously been determined as a general indicator for daily muscle use (Monster et al., 1978; Hensbergen and Kernell, 1997; Langenbach et al., 2004; van Wessel et al., 2005). The present study also determined the daily burst number and length, providing a tool to examine the daily muscle use in more detail. Apart from understanding muscle use, these parameters might also be relevant to increase insight in muscle adaptation as the frequency and level of stimulation are both considered as important factors in determining the fiber type composition (e.g. Ausoni et al., 1990; Pette, 2002).

The differences in burst numbers between the muscles were reflected by the differences in duty time (Fig. 2). In contrast, mean burst length was similar for all muscles. This indicates that differences in duty time between the muscles are mainly determined by variation in burst number and not by changes in burst length. Despite the similar mean burst lengths the distribution curves of the burst lengths, and consequently the median burst lengths, differed considerably between the muscles (Fig. 3). These differences depended on activity level. With increasing activity level, the peaks of the distribution curves showed a shift towards shorter burst lengths, which can be explained by the fact that the high amplitude portion of a burst is generally shorter than its low amplitude portion. Consequently, long bursts present at the 5% level are identified as bursts with shorter duration at higher activity level and most likely represent powerful muscle activation. Short bursts present at low activity levels disappear with increasing activity level and are associated with low level, and thus non-powerful muscle activation.

Shape differences in the distribution curves between the muscles were apparent, especially for activities exceeding the 5% level. At this level the temporalis, deep masseter and digastric showed unimodal distributions, whereas the distributions of the superficial masseter and medial pterygoid were bimodal. The peaks in the curves of the temporalis and deep masseter were found at short burst lengths (0.05 s). As explained above, this suggests that both muscles are predominantly activated in non-powerful motor behaviors of short duration, such as mouth cleaning and grooming, although the temporalis showed many more bursts than the deep masseter. On the other hand, the temporalis also showed a relatively large amount of long bursts (>0.2 s), indicating that this muscle is also involved in behaviors requiring a prolonged low level activity. For activities exceeding the 5% level the distribution curve of the digastric was relatively wide in shape, with a peak number at 0.09 s and a relatively large number of bursts between 0.1 and 0.2 s. For activities exceeding the 20% level the digastric showed a relatively large amount of bursts compared to the temporalis and deep masseter, suggesting that the digastric is more involved in behaviors that require activation at higher levels.

For rhythmic motor behavior, such as mastication, it has been shown that multiple centrally located pattern generators control the contraction patterns of the different muscles (Lund, 1991). The described differences in burst numbers and lengths for various activity levels suggest that the temporalis, deep masseter and digastric are differently controlled during generation of motor behavior. In contrast, the distribution curves of the superficial masseter and medial pterygoid were similar for various activation levels. Although we could not determine a time relation in EMG activity between the muscles, the similarity between the distribution curves could imply that the activation of the superficial masseter and medial pterygoid is commonly generated, both during powerful and non-powerful motor tasks, and that this activation is different from that of the other jaw muscles. The distribution curves for activities exceeding the 5% level showed two peaks (0.05 s and 0.11 s), indicating that the superficial masseter and medial pterygoid are activated using at least two ranges of burst lengths. As explained above, non-powerful motor behavior is presumably responsible for the peak at shorter burst lengths, whereas powerful motor behavior is related to the longer burst lengths at the 5% level. Furthermore, the superficial masseter and medial pterygoid showed a relatively large amount of bursts for activities exceeding the 50% level compared to the other muscles. This implies a larger contribution to powerful behaviors, such as biting and clenching. For the rabbit masseter only it has been reported that the firing pattern of single motoneurons covers a broad range of firing rates and durations (English and Widmer, 2003). Compared to this study we found a wider range in burst durations, which is probably related to the recording of more than one motor unit.

Until now, activity of the jaw muscles has mainly been studied during food uptake (e.g. Schwartz et al., 1989; Weijs et al., 1989; Langenbach et al., 1992; Widmer et al., 2003). Using principal component analysis of the changes in burst amplitude during chewing, Weijs et al. (1999) concluded that the jaw muscles can be divided into three independently controlled groups: (1) the jaw closers, superficial masseter and medial pterygoid; (2) the jaw openers, digastric and lateral pterygoid; and (3) the deep masseter. The present results point to four groups; the same three groups as found in the Weijs study and a fourth group, the temporalis, which was not included in the latter study. Thus these results suggest that muscles are used differently during various behaviors, which could be related to differences in central control of motor behavior between muscles or muscle groups (Weijs et al., 1999; Widmer et al., 2003). Our results also suggest that muscle use depends on the activation level, since the temporalis was the most active muscle during non-powerful behavior while the superficial masseter and medial pterygoid were the most active during powerful behavior. The differences between activation levels could be related to central regulated mechanisms or to peripheral feedback of the muscles (Lund, 1991; Langenbach and van Eijden, 2001).

Muscle activation exceeding the 90% level occurred less than 120 times a day. According to the size principle (Henneman, 1981), only during these powerful bursts are the least easily recruited, fast-twitch and most fatigable units recruited. Consequently, the entire range of activities (>5% level) likely includes recruitment of all different types of motor units, i.e. slow fatigue resistant motor units as well as fast and

fatigable motor units. If this principle is applied to the present results it can be speculated that the large burst numbers of the temporalis and deep masseter at low activity levels require many relatively fast units, which are not necessarily fatigue-resistant because of the short duration of their contractions. In contrast, the longer bursts of the digastric, including all activities (>5%), would require more fatigue-resistant units, whereas the superficial masseter and medial pterygoid would require a mixture of fast and slow units, resulting from their bimodal distributions for activities exceeding the 5% level. High duty times imply prolonged muscle activity and this has been associated with large percentages of slow fatigue-resistant fiber types (Monster et al., 1978; Kernell and Hensbergen, 1998). Although this might be true, the detailed characterization of muscle activity presented in the present study shows that high duty times can also be generated by large numbers of short bursts (see temporalis) and thus could be related to large percentages of fast fiber types. The differences in burst length distribution between the deep and superficial masseter are in line with reported differences in histochemical and physiological properties between these muscle regions, indicating that the deep masseter contains more fast type units than the superficial masseter (English et al., 1999; van Eijden and Turkawski, 2001).

In a previous study (van Wessel et al., 2005) we found that the duty time of the jaw muscles in rabbits did not change during maturation. The present study revealed that burst number and burst length were also unchanged 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 muscle cross-sectional area (Weijs et al., 1987), and substantial changes in fiber type composition (Bredman et al., 1992; Eason et al., 2000; English and Schwartz, 2002). Despite these anatomical changes, the mastication pattern of young animals resembles that of adults (Weijs et al., 1989; Langenbach et al., 1992). Thus although timing and coordination between muscles are improved during maturation, the pattern of contraction is established long before the anatomical changes have completed.

Although duty time did not change during maturation, we reported, for activities exceeding the 5% level, a significant decrease in the interindividual variation in duty time for the digastric and the superficial and deep masseter (van Wessel et al., 2005). Since variation in duty time is associated with variation in burst number it can be expected that the interindividual variation in burst number is also reduced during maturation. This reduction in interindividual variation was indeed found for burst number and also for burst length, for all muscles except the medial pterygoid (data not shown). This decrease in interindividual variation could be related to a reduction in neuromuscular plasticity during maturation (Kernell, 1998). Muscles are susceptible to an adaptive range in which muscle properties can adapt through alterations in use. During maturation this adaptive range decreases, not only by changes in central control, but also by alterations in afferent feedback mechanisms (Westerga and Gramsbergen, 1993).

In conclusion, differences in duty time between muscles are mainly caused by variation in burst number and not burst length. Activation of the jaw muscles is differently controlled during powerful and non-powerful motor behaviors, for at least four different muscle groups. In addition, burst number, burst length and duty time of the jaw muscles do not change during maturation from 9–14 weeks, indicating that functional organization of motor control patterns does not change during this period.

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