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Temporal Dynamics of Human Masticatory Sequences

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GERSTNER, G. E. AND T. CIANFARANI. *Temporal dynamics of human masticatory sequences.* PHYSIOL BEHAV **64**(4) 457–461, 1998.—Many motor behaviors produced by humans and other mammals are temporally segmented. That is, sequences of rhythmic or repetitive behavior occur as a series of brief, 2- to 4-s bouts separated from each other by pauses or posture adjustments. Little is known about the physiological mechanisms underlying temporal segmentation, although several hypotheses have been advanced. Experimental and modeling studies are currently underway to gain insight into this phenomenon. One of the problems hampering advancement is the lack of relatively simple behavior models that can be studied in both humans and other mammals. We have recently reported that temporal segmentation occurs in guinea pig chewing sequences. Thus, it seems logical to explore whether temporal segmentation occurs in human chewing sequences as well. Toward this end, the current study evaluated the temporal dynamics of chewing sequences in humans. Thirteen subjects were videotaped on campus eating areas during lunch-time. Inter-occlude intervals, i.e., time between maximum jaw closures, were calculated using a custom computer program, which also recorded whether the interval represented a chew or a pause in chewing. Chewing rate, pause durations, and chewing burst durations, i.e., duration of continuous chewing uninterrupted by pauses, were calculated. Median chewing burst duration for the sample was 2.91 s. This corroborates other studies' findings of 3-s temporal segmentation in repetitive movements. We conclude that automatic chewing sequences contain temporal segmentation. Future work is required to gain insight into whether the physiological mechanisms of this time-based phenomenon are similar among different species.   © 1998 Elsevier Science Inc.

Mastication   Chewing rate   Chewing burst   Temporal segmentation   Human

MANY movement patterns in humans (3,15,20,24–26) and other mammals (4,5,12,16) are partitioned into 2- to 4-s segments. Movements characterized by this temporal segmentation include repetitive and non-repetitive behaviors (3–5,9,12,15,16,24–26, 28,29). The segmentation is particularly apparent in repetitive movement patterns, like squirrel locomotion, where an otherwise continuous movement sequence is partitioned by pauses or posture adjustments into a series of 2- to 4-s bouts (3–5).

A similar 2- to 4-s structure occurs in perceptual phenomena (6,20–22) and short-term or working memory (1,15,21). This has led to the hypothesis that perception, short-term memory, and movement patterns share a mechanism that structures the otherwise continuous processing of neural information into short-duration units (6,21,24,25). A related hypothesis is that 2–4 s is the time required by the nervous system to integrate neural information into a "Gestalt" (24). That is, it takes 2–4 s for the nervous system to articulate, bind, and integrate motor or perceptual elements into functionally coherent units.

The physiological nature of temporal segmentation is poorly understood (20–22). The hypothesis that temporal segmentation is disrupted in psychoses (3,5,6,9) suggests a link between physio-logical systems subserving segmentation and neural systems affected by psychoses. Our work with guinea pig mastication, a behavior that manifests temporal segmentation (5,9), provides support for this hypothesis in that temporal segmentation features are altered in animals injected with haloperidol or apomorphine (9; unpublished observations).

Our long-term goals are: a) to develop animal models of temporal segmentation in order to investigate its underlying proximate mechanisms, b) to study temporal segmentation in human disease states to confirm that the mechanism in humans is biologically similar to that seen in animals, c) to develop mathematical models to understand the dynamics and "emergent" properties of the mechanism generating the segmentation, and d) to determine whether temporal segmentation plays a general role in motor and perceptual planning and sequencing (cf. 8,12,13).

Toward these ends, we have been evaluating oral behavior patterns for the presence of temporal segmentation. This stems from our familiarity with oral behaviors (2,5,7,9,10). But more importantly, because oral stereotypies accompany psychoses and their treatment (3,5,6,9), and because these stereotypies appear to lack normal temporal segmentation (3), it seems that oral behavior

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represents a potentially useful assay for studying temporal segmentation. Furthermore, we have already reported the existence of temporal segmentation in an animal model of oral behavior (5).

To date, little work has focused on segmentation in rhythmic oral motor behaviors in humans (cf. 28,29). We hypothesized that this was because oral motor behaviors have been studied in contrived settings where natural intermittency may be overridden by conscious control. Therefore, we proposed to study human chewing sequences in natural settings in order to ascertain whether temporal segmentation of oral behavior would occur under such conditions. Thus, the purpose of the current study was to determine whether there was evidence of temporal segmentation in human mastication, and if so, to quantify and compare it to temporal segmentation reported in previous studies.

MATERIALS AND METHODS

Subjects

The study consisted of 10 females and 3 males, ~19–28 years of age. Subjects included undergraduate university and dental students eating outdoors at public facilities on the University of Michigan campus. Subjects were videotaped without their awareness. Protocols for the study were approved by the appropriate institutional human subjects review board, and subjects' anonymities were fully protected.

Experimental Setup

Subjects were videotaped (Olympus Digital S-VHS Camcorder, Model VX-S405, 4× teleconversion lens) from upper floors of campus buildings overlooking popular outdoor eating areas. Taping occurred between 1100–1300. Taped individuals had to be facing the camera ($\pm 30°$), and their mouths had to be clearly visible in the camera viewfinder. Taped subjects were engaged primarily in eating as opposed to socializing, studying, or other non-eating behaviors. Subjects also had to be unaware of the camera's presence or of the fact that they were being videotaped. Subjects meeting these criteria were taped continuously for at least 3 min.

Camera aperture was stopped down to increase depth of field. Camera digital shutter speed was increased to minimize blur. Also, due to the significant magnification of the teleconversion lens, the camera was attached to a tripod and not touched once taping began. These procedures assured that the sharpest possible images would be obtained for scoring purposes.

Data Acquisition

Videotaped chewing data were digitized with software developed in the laboratory. Digitization methods have been described elsewhere (10). Briefly, videotaped data segments were observed at slow speeds, and a single investigator pressed "Return" on a computer keyboard whenever subjects' maximum jaw closures occurred on the videotape. A computer program kept track of the time between successive Return key strokes; this time will be referred to as the inter-occlude interval (IOI). Obviously, if a subject was chewing, then the IOI represented the duration of a chew. By the same token, if a subject had paused chewing, then the IOI represented the duration of a pause. Between successive Return key strokes, the investigator could enter whether the subject's mouth was difficult to see. Data segments containing difficult-to-see chewing sequences were not analyzed.

Intra-rater reliability at identifying maximum jaw closures was ~ 97%. Inter-rater reliability at identifying maximum jaw closures was >95%. However, data analyzed in the study represented those scored exclusively by only one investigator.

Data Analysis

Based on observations of the videotaped data, and data we have previously obtained (7,10), we established that all chews were <1.5 s in duration and that >95% of all pauses were ≥1.5 s in duration. Hence, IOIs < 1.5 s defined chews, whereas IOIs ≥ 1.5 s defined pauses. Chewing burst durations were defined as the cumulative duration of consecutive IOIs with values <1.5 s.

Because data recording often began and ended in the middle of an IOI, the initial and final IOIs were excluded from mean chew or pause duration calculations. Likewise, if a data record's initial or final IOI was a chew, i.e., its duration < 1.5 s, then it was likely that the data record began or ended in the middle of a chewing burst. Such initial or final chewing bursts were excluded from mean chewing burst duration calculations, because they were assumed to be incomplete.

Using the 1.5-s cutoff and the exclusionary criteria just described, a computer program developed in the laboratory identified chews, pauses, and chewing bursts in the data sequences for each subject. Chew durations were normally distributed; hence, means and standard deviations were calculated for these data (BMDP 2D, BMDP Statistical Software, Inc., Los Angeles, CA, USA). Pause and burst durations were not normally distributed; hence, medians and standard errors of the medians were calculated for these data (BMDP 2D). Standard error of the median was calculated as follows:

$$SEMed = (x_i - x_j) \div (2\sqrt{3})$$

where x_i and x_j were the i-th and j-th values of the ordered data set, respectively. The integers, i and j, were determined by calculating the integer part, i.e., truncating $1 + [(n + \sqrt{3n}) \div 2]$ and $1 + [(n - \sqrt{3n}) \div 2]$, respectively, where n = sample size.

RESULTS

Videotaped chewing occurred in rhythmic bouts. Chewing bouts were typically bounded by pauses, during which times chewing ceased and other behaviors occurred. Some of these behaviors involved the oral apparatus, viz., swallowing, incising, licking lips, talking, or using the tongue to manipulate food or clean teeth. Other behaviors did not involve the mouth actively, viz., vigilance or cessation of all oral movements. Precise incidences of these behaviors were not calculated due to ambiguities in differentiating between some of the categories. However, ~70% of the pauses represented swallowing, incising, licking lips, or using the tongue to manipulate food or clean teeth. The remaining 30% represented vigilance, cessation of all oral movements, or talking.

Table 1 shows results reported by subject. The table shows chewing cycle duration means (1 SD), pause duration medians (1 SEMed), and chewing burst duration medians (1 SEMed) (see Materials and Methods). Also shown are the sample sizes (n) used in calculations. The table provides an indication of the variation in the data among and within subjects.

Figure 1 plots statistics of chewing cycle, pause, and chewing burst durations for the entire subject group. The figure shows the mean (1 SD) chew duration, the median (1 SEMed) pause duration, and the median (1 SEMed) burst duration for the group. Results in Table 1 and Fig. 1 indicate that chew durations were longer than those reported under laboratory conditions (18,23).

TABLE 1

STATISTICAL RESULTS BY SUBJECT

	Chewing cycles			Pauses			Chewing bursts		
Subject	n	Mean	SD	n	Median	SEMed	n	Median	SEMed
1	77	1.13	0.17	13	2.01	0.61	13	5.28	2.36
2	51	1.20	0.15	16	2.05	0.29	12	3.57	1.94
3	30	1.01	0.23	21	2.20	0.33	12	1.82	0.68
4	31	1.05	0.23	23	2.58	0.39	10	3.12	0.49
5	46	1.20	0.17	13	1.75	0.79	8	2.42	4.89
6	43	0.93	0.22	12	3.54	2.50	8	4.33	1.39
7	51	1.10	0.18	10	2.42	1.98	8	5.97	2.80
8	38	1.04	0.22	19	1.82	0.59	13	2.33	0.44
9	41	1.18	0.27	18	2.68	0.65	12	3.26	1.00
10	71	1.15	0.18	11	2.28	0.79	9	9.67	4.34
11	39	1.18	0.18	21	1.73	0.27	14	2.55	0.93
12	16	1.09	0.38	15	2.01	1.26	6	2.94	1.07
13	37	1.07	0.18	17	1.98	1.62	13	1.40	0.61

FIG. 2. Frequency histogram of chewing burst durations of all subjects combined.

Pauses have not been reported in the masticatory literature; hence, quantification of this feature is new. The median chewing burst and pause durations (Table 1, Fig. 1) were similar to the median duration of other temporally segmented behavior units previously reported in human (3,15,20,22,24–26,28,29) and animal (4–6,9, 12,16) studies.

Figure 2 is a frequency histogram of chewing burst durations. Analyzable chewing bursts were found in all 13 subjects' data records (Table 1). This meant that rhythmic chewing bursts were typically bounded by pauses, during which time chewing ceased. The shortest "bursts" were made up of single chews. Single-chews occurred 27 times. The longest burst consisted of 22 consecutive chews. About 67% of the sampled chewing bursts were ≤4 s in duration and made up of 1–4 chews each.

Figure 3 shows a scatterplot of burst duration versus the number of chews making up the given burst. The plot pools data for all subjects. Note linear regression results, top of figure. Most rhyth-

mic or repeating human behaviors characterized by temporal segmentation show a phenomenon termed pre-syntactical motor planning (12,16). Pre-syntactical motor planning occurs when the number of repeating behavior units in a burst minimally affects burst duration. This occurs because the frequency of the rhythmically recurring units is modulated to compensate for the number of units in a burst (12,16). If pre-syntactical planning existed in mastication, then a considerable increase in the number of chews in a burst should be accompanied by only a slight increase in burst duration. The exponential function drawn in Fig. 3 approximates the curvilinear path along which data points should be scattered if pre-syntactical motor planning were an integral part of chewing bursts.
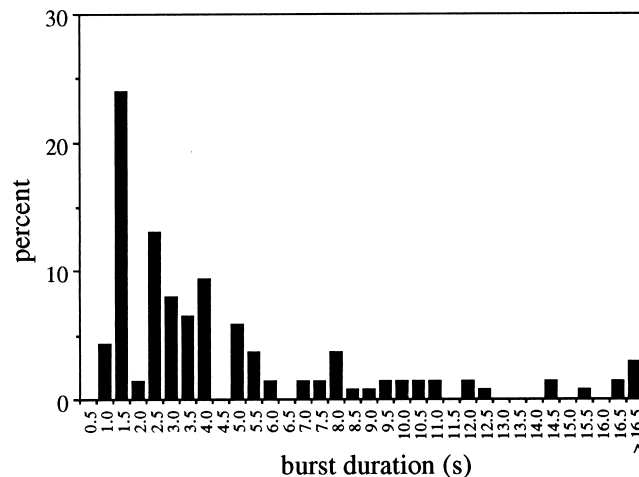
In the absence of pre-syntactical motor planning, chewing rate should be independent of burst duration. Consequently, burst duration and the number of chews making up the burst should be directly correlated. The linear relationship evident in Fig. 3 indicates that pre-syntactical motor planning did not occur in this masticatory data.
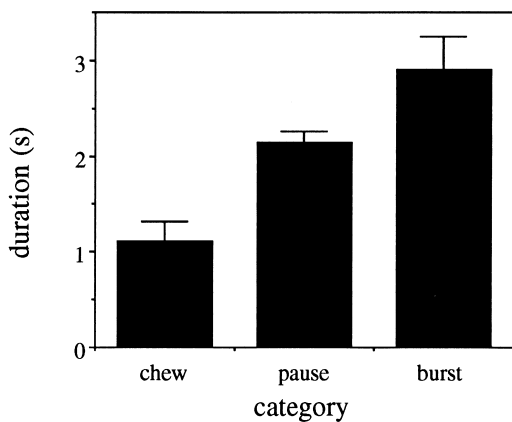

FIG. 1. Mean chew duration, median pause duration, and median chewing burst duration. Error bars = 1 SD for chew duration and 1 SEMed for pause and burst durations. Results based on pooled data from all 13 subjects, viz., 571, 209, and 138 observations, respectively (Table 1). Abbreviations: SD = standard deviation, SEMed = standard error of the median (see Materials and Methods).
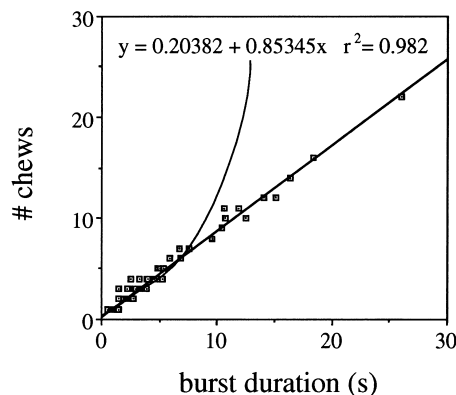

FIG. 3. Scatterplot and linear regression analysis results of burst duration vs. number of chews in the respective burst.

$$y = 0.20382 + 0.85345x \quad r^2 = 0.982$$

DISCUSSION

This study evaluated and analyzed temporal aspects of human mastication under uncontrolled conditions. Mastication under such conditions occurs in complex sequences with other behaviors, e.g., talking, drinking, swallowing, incising, etc. How such sequencing affects chewing parameters has not been evaluated, because controlled studies reduce the probability that non-masticatory behaviors will occur. However, neural mechanisms governing masticatory burst onset, maintenance, and cessation must integrate mastication with other behaviors to create complex behavior sequences. The importance of understanding the physiology of behavior sequencing has long been appreciated (13); however, the mechanisms governing sequencing remain poorly understood. We, therefore, argue that an evaluation of mastication under routine conditions provides insight regarding the nature and control of complex motor sequences.

The results revealed that temporal segmentation or intermittency was common to all subjects' data sets. This differs from results obtained under controlled laboratory settings (e.g., 14,27), where complete and relatively long-duration (>10 s) masticatory sequences begin with food acquisition and end when the food bolus is swallowed. In the current study, chewing sequences were often interrupted by other behaviors. Most often, these interruptions were probably associated with tongue repositionings of food, pauses in oral movements, and swallowing a piece of the food bolus. But occasionally speaking bouts and other rarer behaviors intervened. Under such conditions where complex behavior pattern sequences emerged, chewing bursts were relatively short (~ 3 s).

To our knowledge, this temporal segmentation is a new reporting for human mastication. However, similar segmentation has been reported for a variety of rhythmic or repetitive behaviors in humans (3,24–26,28,29). It has also been found in over 160 behavior patterns in at least 23 mammalian species (4–6,8,9,12, 16, also unpublished observations). Temporal segmentation is also found in deaf-blind children, providing evidence for an endogenous mechanism that controls behavior burst onsets and offsets (15). Thus, 3-s segmentation appears to be a common feature of mammalian behavior patterns, including human mastication.

Obviously, humans and animals can perform a given motor behavior for time periods > 3 s. However, during such extended repetitive motor acts, segmentation frequently remains evident as "very slight changes in the movement patterns or very short interrupting pauses" (3). We suggest that the equivalent in human chewing sequences would be: a) shifting the chewing side from left to right or vice versa; b) repositioning the food bolus with the tongue or cheeks; or c) cleansing teeth with the tongue. Such movements would protract a given chew's duration, cause a brief pause, or possibly change the movement pattern in detectable ways. Our observations of the videotaped data demonstrated that this was, indeed, the case. This is the reason it was practical to use the 1.5-s cutoff to differentiate chews from pauses (see Materials and Methods).

Our investigations of humans chewing under laboratory conditions suggest that segmentation rarely occurs here. We have used the 1.5-s cutoff on data obtained from subjects ($n = 60$), who were asked to chew gum in a laboratory-based study. Temporal segmentation was almost undetectable in these data sets, occurring only 1–2 times in $< 25\%$ of the subjects (unpublished observations). This indicates that temporal segmentation may be sensitive to some environmental conditions. These unpublished findings may also explain why segmentation has not been reported in previous mastication studies.

Previous work has reported temporal segmentation in talking

(28,29) and vigilance (6). Because some of the pauses documented in our current sample represented "bouts" of talking or vigilance, the issue emerges as to whether the temporal segmentation in chewing was simply the result of chewing's association with other "naturally" segmented behaviors. Although this is a legitimate alternate hypothesis, at least three lines of reasoning refute it. First, segmentation in our chewing samples was associated with at least five other behaviors aside from talking and vigilance (see Results). It seems unlikely that all of these behaviors would be naturally segmented, and that chewing would be the only one not naturally segmented.

Second, chewing and some of the behaviors, e.g., vigilance, were not physically mutually exclusive. That is, they did not use the same muscles or articulations in mutually exclusive ways. Given the massively parallel neuromotor systems of humans, it is intriguing that behaviors that are not mutually exclusive occurred serially instead of in parallel. This implies that there are constraints on the information and motor production capacity of the nervous system, and that temporal segmentation is a manifestation of these constraints. Several previous papers have presented similar arguments (3,8,24). Future studies will need to evaluate this issue more closely.

Third, it is important to recognize that chewing is a motor behavior that must be actively produced by brain stem mechanisms and modulated by suprabulbar inputs (11,14). In other words, chewing must be actively switched on and off. Hence, behavior sequences that alternate between chewing bouts and other behaviors must either be actively controlled or be an emergent property of a mechanism that plays a role in organizing such sequences. Therefore, chewing probably does not simply fill in gaps, because it must be actively inserted and articulated with other behaviors. Future modeling and experimental studies (see Introduction) will evaluate these issues more fully.

Previous studies have reported a coupling between the rhythmicity of a given motor act and the number of times the motor act is repeated in a given burst (12,16). This coupling, referred to as pre-syntactical motor planning (12), is such that the number of repetitions of a motor act in a given burst does not affect the duration of a burst in a linear way (12,16). Rather, the more repetitions of a motor act within a burst, the faster the rhythmicity of the act. Interestingly, pre-syntactical motor planning appears only in human and chimpanzee behaviors and does not appear in other primates or mammalian species (5,12,16). However, the results reported in this paper suggest that human masticatory bursts do not possess pre-syntactical motor planning either.

Most human behaviors characterized by pre-syntactical motor planning are voluntary behaviors as opposed to automatic behaviors (3). Because chewing is largely automatic under routine conditions (14,17–19), perhaps this is a reason why pre-syntactical motor planning was not observed in our study. However, our unpublished findings suggest that voluntary mastication possesses neither pre-syntactical planning nor temporal segmentation. Hence, automatic and voluntary mastication may represent behaviors that are unique in the human repertoire with respect to pre-syntactical motor planning and temporal segmentation.

In summary, the current study found evidence of temporal segmentation in human mastication under routine conditions. This temporal segmentation, like the temporal segmentation reported in other human behaviors, was characterized by rhythmic chewing bouts of $\sim$3-s duration separated from each other by brief "pauses." Although the physiological nature of temporal segmentation is unknown, physiological studies into its nature will require a useful behavior model. Because much is known about the bulbar mechanisms that generate chewing (11,14), and because many diseases disrupt oral movements and temporal segmentation in oral behav-

ior (3,9), we believe chewing represents such a potentially useful paradigm. Future work will determine why temporal segmentation is diminished in voluntary chewing, what physiological mechanisms generate it, what its dynamic nature and behavioral implications are, and whether its disruption plays a key role in neurological or psychological disorders.

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