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SYMPOSIUM

Ontogenetic Changes in Mammalian Feeding: Insights from Electromyographic Data

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Synopsis All infant mammals make a transition from suckling milk to eating solid foods. Yet, the neuromuscular implications of the transition from a liquid-only diet to solid foods are unknown even though the transport and swallowing of liquids is different from that of solids. We used legacy electromyography (EMG) data to test hypotheses concerning the changes in motor pattern and neuromuscular control that occur during the transition from an all-liquid diet to consumption of solid food in a porcine model. EMG signals were recorded from five oropharyngeal muscles in pigs at three developmental stages (infants, juveniles, and adults) feeding on milk, on food of an intermediate consistency (porridge), and on dry chow (juveniles and adults only). We measured cycle frequency and its variation in "transport cycles" and "swallow cycles". In the swallow cycles, a measure of variation of the EMG signal was also calculated. Variation in cycle frequency for transport and swallow cycles was lowest in adults, as predicted, suggesting that maturation of feeding mechanisms occurs as animals reach adulthood. Infants had lower variation in transport cycle frequency than did juveniles drinking milk, which may be due to the greater efficiency of the infant's tight oral seal against the teat during suckling, compared to a juvenile drinking from a bowl where a tight seal is not possible. Within juveniles, variation in both transport and swallow cycle frequencies was directly related to food consistency, with the highest variation occurring when drinking milk and the lowest when feeding on solid food. There was no difference in the variation of the EMG activity between intact infants and juveniles swallowing milk, although when the latter swallow porridge the EMG signals were less variable than for milk. These results suggest that consistency of food is a highly significant determinant of the variation in motor pattern, particularly in newly weaned animals.

Introduction

Adult mammals represent a wide-range of feeding diversity: including generalists and specialists, the latter of which include ruminants and carnivores. Yet, all infant mammals utilize the same feeding mechanism—suckling their mother's milk. Karen Hiiemae developed the Process Model of Feeding (Hiiemae and Crompton 1985) as a framework for understanding the physiological relationships among the different functions that occur during normal feeding. For both solid and liquid food, these functions can include: acquisition, stage I intraoral transport, mastication and manipulation, stage II intraoral transport, aggregation of the bolus, and swallowing. The process model for suckling in infant mammals is simple compared to the adult process model which has to allow for the processes associated with the manipulation and physical reduction of solid food.

Infants have two basic types of cycles: suck/transport cycles and suck/transport cycles with an embedded swallow i.e., suck–swallow cycles (German and Crompton 2000). The adult process model involves cycles that include multiple specific

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functions, including transport, mastication, and swallowing (Hiiemae and Crompton 1985; Hiiemae 2000). For this article, we have simplified these into (1) transport/processing cycles, in which these two behaviors can occur in the same cycle and (2) cycles containing a swallow, and which we term "swallow cycles" (Hiiemae 2000).

All mammals share the transition from simple feeding by infants to this more complex behavior of adults (German and Crompton 2000). The eruption of the deciduous dentition, in general, heralds the change from suckling, and the consumption of only liquids, to the consumption of semi-solid and solid foods. This ontogenetic process, termed weaning, has important neuromuscular implications, beyond the introduction of acquisition and mastication to the food-processing system. First, the transport of solid food, through the oral cavity into the oropharynx is mechanically different from the transport of liquid through the same space (Hiiemae et al. 1978; Hiiemae and Crompton 1985). Second, the successful movement of food into, and only into, the esophagus, becomes critical when solid boluses are involved. Aspiration, or failure to protect the airway during a swallow, is problematic with liquids because of the potential for aspiration leading to pneumonia. However, aspiration of solid foods, is more serious, because it can result in complete blockage of the airway, asphyxiation, and death. As such, the need for more precisely timed swallows becomes acute at the time of weaning.

Changes in the motor pattern occur when individuals make the transition from suckling (head-up in all mammals) to drinking from a bowl or natural water source (head-down in most mammals) (Thexton et al. 1998). Yet the changes in motor pattern and neuromuscular control that may occur during the transition from a liquid diet to solids are not known. In particular, the neurophysiologic differences between transport cycles as compared to cycles that contain a swallow are not well understood.

We investigated the ontogenetic changes that occur in feeding, using a porcine model and existing/legacy electromyography (EMG) data to compare motor patterns during the processing of food. In order to quantify the constancy of neuromuscular control of oral function, we calculated measures of: (1) variation in the frequency of occurrence of intraoral transport (transport cycles) and swallowing (swallow cycles) and also (2) variation in the pattern of EMG activity during swallow cycles.

Control of a bolus during swallowing is critical for the prevention of aspiration and its potentially fatal sequelae. Since intraoral transport includes cycles with multiple functions depending on type of food (e.g., suck/transport for milk versus acquisition, transport, and mastication cycles for solid foods) we hypothesize that these cycles will be highly variable. Milk is a relatively homogeneous fluid with low variability compared to the more heterogeneous solids in this study. As such, it is expected that given the dangers of asphyxiation due to aspiration of a solid bolus, there would be less variation in the motor response for consumption of solid food, relative to liquid food, in an effort to ensure tight control of a solid bolus.

Studies of motor learning have demonstrated that novel behaviors are characterized by decreased efficiency and higher variability than previously known behaviors (Shadmehr and Wise 2005). Thus, we also expect that the motor patterns of older individuals with prior experience with a given food will be characterized by lower variation in cycle frequency during feeding than is true for younger individuals.

We tested three hypotheses (1) that the frequency of intraoral transport cycles is more variable than for swallow cycles at any age, (2) that the patterns of EMG activity and cycle frequency are less variable for either semi-solid or solid food than for liquids at a given age, and (3) that variation in cycle frequency decreases with age, from infants to juveniles, and then from juveniles, who have just begun to eat solid food to adults who have previously learned to handle such food.

Materials and methods

Experimental subjects and feeding procedures

A porcine animal model of feeding was appropriate for this study because pigs are tractable in a laboratory setting, are easy to train, eat readily, and can be acquired at different developmental stages. The porcine model for feeding has been successfully validated and used for nearly 40 years (Herring and Scapino 1973; German et al. 1992, 1998). The data in this article were collected as part of a large set of experiments, some of which have been previously published (Thexton et al. 2007). All the data used in this article followed from studies using previously published surgical procedures and experimental protocols.

This article used data from pigs of three ages. Five of these pigs were 5–14 days old and lacked most postcanine dentition ("infants"). Three pigs were 35-days old and had postcanine dentition ("juveniles"). A third group included two pigs that had full adult dentition and were 9-months old ("adults"). The adult pigs had been weaned prior to arrival. For comparative purposes, previously published data from decerebrate pigs (Thexton et al. 2007) have also been included in this study.

Infant pigs were fed milk from a modified baby bottle with an elongated soft nipple (Nasco, Fort Atkinson, WI, USA). Juvenile pigs were fed milk from a bowl and were sequentially introduced to chow porridge (a mixture of 1 cup of dry chow and 1 cup of milk replacer blended to oatmeal consistency in an electric blender) and dry chow from a bowl. Adult pigs were fed dry chow and porridge from a bowl.

Surgical procedure and recording of data

Fine-wire bipolar EMG electrodes were surgically inserted in up to 15 muscles per individual. Those analyzed in this study were common to all individuals and included: anterior belly of the digastric, geniohyoid, sternohyoid, hyoglossus, and omohyoid muscles. A detailed schematic of the muscles used for this study and the known force vectors associated with those muscle can be found in the supplemental figure. Animals were otherwise intact, healthy specimens characterized by normal development and behavior.

Animal husbandry and experimental procedures were performed in accordance with Harvard University IACUC approved protocol numbers 21-02 and 23-05. The data included in this study were obtained over a period of 3–7 days for each animal. EMG signals were amplified (×400 to ×10000) using an MA-300 EMG System (Motion Lab Systems Inc, LA, USA) with a band pass of 20 Hz to 2 kHz and a 60 Hz notch filter, and then recorded on a TEAC RD-145 T digital data recorder at 6 kHz.

Experimental design, processing, and analysis of data

The experimental design for the current study included three fixed factors (type of food, type of cycle, and developmental stage) and a single random factor (individual). Animals were grouped by developmental stage (infants, $n = 5$; juveniles, $n = 3$; adults, $n = 2$) based on feeding history and dentition. The model was incomplete (i.e., we did not have all food types for each age group). The factor "food type" had three levels: milk (infants and juveniles), chow porridge (juveniles and adults), and dry chow (juveniles and adults). The factor "cycle type" had three levels: transport/processing, swallowing, and acquisition (for solid food only), as described below.

Previous analyses, that included integrated imaging and EMG data, showed a qualitative difference in EMG activity between transport cycles and cycles that contained a swallow (Thexton et al. 1998). We identified transport/processing cycles using geniohyoid or hyoglossus EMG signals, depending on available electrodes in a given animal, and signal quality within these muscles. Swallow cycles were identified using omohyoid EMG signals. We used sequences in which clear bursts of the EMG signal for the appropriate muscle developed from a nonnoisy baseline.

Cycle frequency was calculated for each individual for each food type and applicable cycle type (transport/processing and swallowing for all food types). This was done by counting the number of swallows within a feeding sequence over a duration of time. In the case of transport/processing cycles, we counted the number of cycles that occurred within a specific time period. We selected periods during which no swallow cycles occurred. The beginning of the time period was the time at which the muscle in question first reached 20% of its maximum EMG activity, and the end was taken as the time when the last cycle reached 20% of its maximum. The cycle frequency was the number of cycles divided by the period of time in which they occurred.

Swallow cycles were easily distinguished by the level of EMG activity in the omohyoid muscle (Thexton 1996; Thexton and German 2001). We counted the number of swallow cycles within a time interval of 5–6 s for infants (as they fed for shorter periods of time), and within a time interval of 10–20 s for juveniles and adults. Thus, our unit of analysis was an interval for which we calculated cycle frequency. There was a total of 481 such intervals for the data on cycle frequency.

To measure variation in cycle frequency, we measured the variation within each of our treatment groups defined by our two factors, age and food type. We had three factors: (1) cycle type, with levels "transport" and "swallow"; (2) age, with levels "infant", "juvenile" and "adult"; and (3) food type, with levels "milk", "porridge", and "solid". However, because the infants only drank milk, and we had only soft solid and solid data for adults, we had only 12 age–food type groups.

We used interquartile range (IQR) as a measure of simple variation within each of these groups. We tested for differences in cycle frequency using a multifactor mixed model. All hypothesis testing for specific contrasts was done with Bonferoni corrections. No calculation of significance in differences in variation was possible because we did not have multiple measurements of variation for each group.

We also measured the variation of the EMG signal, itself, for the five muscles in common between infants and juveniles: the anterior belly of digastric, geniohyoid, sternohyoid, hyoglossus, and omohyoid muscles. Adult EMG data required additional processing and were unavailable for this article. For these data, 5-s windows of EMG data were extracted and imported into a data-processing program called SEQUENCER (written by David Hertweck, and available from the authors). The program rectifies, integrates (across a 10-ms reset interval) and performs baseline correction on all sequences (Thexton et al. 2007). Individual cycles of data were identified, using the same signal for all members of an age group (e.g., omohyoid for juveniles). Then, a set of cycles for each of the muscles (using the same time basis) were turned into a matrix, indexed by each integration-reset interval, with scaled EMG signal as the values. The first, second, and third quartiles of EMG activity were calculated for each named muscle in each group. From this, the IQR and median level of activity were obtained for each time bin across an entire cycle (duration = 100 scaled units). We then calculated Index of Signal Variability (Equation 1). It is a single number that represents the variation in a set of EMG signals which in turn permits comparison of variation between EMG signals (Thexton et al. 2007).

$$\text{Index of Signal Variability} = \frac{\sum_1^n \text{Interquartile Range}}{\sum_1^n \text{Median Activity}} \qquad (1)$$

We also included published results for EMG patterns in decerebrate infants (Thexton et al. 2007) because a comparison between decerebrate and intact infants could provide insight into the cerebral control of transport/processing or swallowing. We compared our groups for differences due to age–food type for swallows using a one-way ANOVA, with four levels: "decerebrates," "infants," "juveniles (milk)" and "juveniles (porridge)".

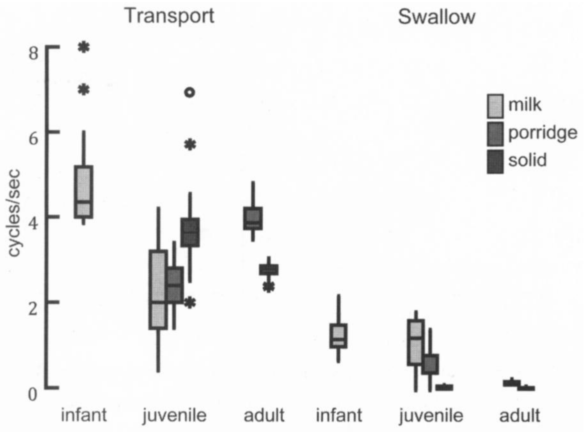

Fig. 1 Cycle frequency (in cycles/second) for transport (left) and swallow cycles (right) for infant, juvenile, and adult pigs eating milk (light gray), porridge (dark gray), and solid chow (black). Each box represents the IQR of the data, with the horizontal line representing the median for that treatment. The whiskers represent the range of the data that are within 1.5*IQR. The values of significant outliers are indicated by asterisks (above the upper quartile or below the lower quartile by > 1.5 IQR) and open circles (above the upper quartile or below the lower quartile by >3.0 *IQR) respectively.

Results

Cycle frequency

In the case of milk, the infant pig generated transport cycles at a higher frequency than did juveniles ($P < 0.001$, Fig. 1). When ingesting and transporting porridge consistency food, juveniles exhibited lower frequency cycles than did adults. However, when transporting solid food, adult pigs generated lower frequency cycles than did juveniles transporting solid food ($P < 0.001$, Fig. 1). There was no difference between transport cycle frequency when juveniles consumed either milk or porridge. There was no significant difference in the frequency of swallowing associated with the type of food consumed (milk, porridge, chow) between sequentially paired age groups ($P > 0.6$, Fig. 1) i.e., infants and juveniles swallowed milk at the same rate, and juveniles and adults swallowed porridge and solid food at the same rate. However, within juveniles, the frequency of milk swallows was higher than for porridge swallows, which in turn was higher than for swallowing solid food ($P < 0.05$, Fig. 1).

For all types of food, the variation in cycle frequency (as measured by IQR) shown by juveniles was greater than that shown either by infants (milk) or by adults (porridge and solid food). This was true for both transport and swallow cycles (Fig. 2). For juveniles, the most variable cycle frequencies occurred when consuming milk, followed by porridge, with solid food being associated with the least variable frequencies. Variation in transport cycle frequencies was higher for every age–food combination than the variation in frequencies of swallowing (Fig. 2).

Index of Signal Variability for EMG of swallow cycles

The Index of Signal Variability for EMG signals occurring during swallowing was significantly greater

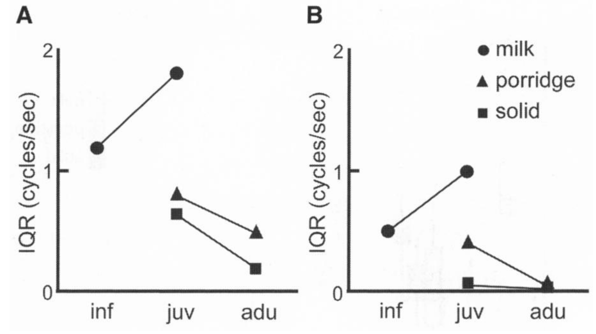

Fig. 2 IQR for transport cycles (**A**) and swallow cycles (**B**) for infant (inf), juvenile (juv), and adult (adu) pigs eating milk (circles), porridge (triangles), and dry chow (squares).

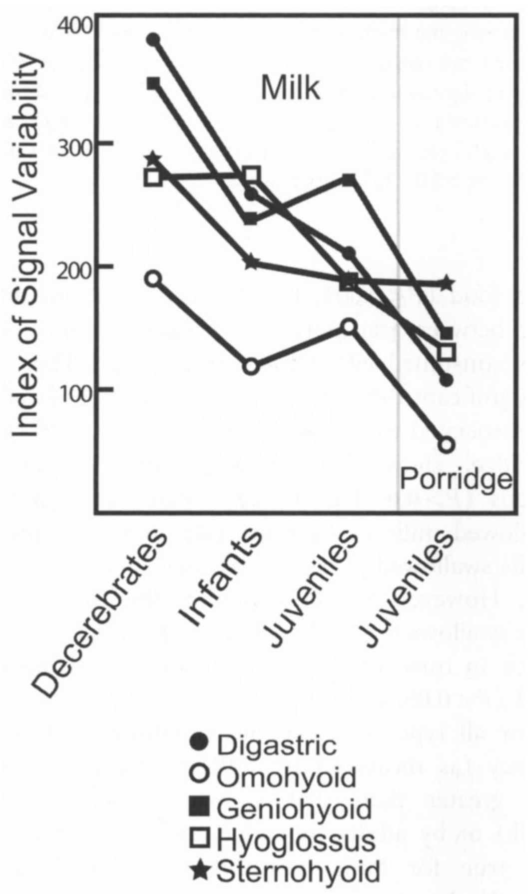

Fig. 3 Index of signal variability (ISV) during swallowing for five muscles of the swallowing apparatus: anterior belly of digastric (closed circle), omohyoid (open circle), geniohyoid (closed square), hyoglossus (open square), sternohyoid (star). Values were calculated for juveniles drinking milk or eating porridge. Previously published data for decerebrate and intact infant pigs drinking milk are included for comparison (Thexton et al. 2007; German et al. 2009). Although, there is spread in variation within each age group, a significant pattern emerges. Variation is highest in infants drinking milk and lowest in juveniles consuming porridge consistency food ($P<0.01$). There was no statistical difference in ISV between infants and juveniles drinking milk.

($P<0.01$) in decerebrate infants than in intact infants (Fig. 3). The Index of Signal Variability did not differ between swallow cycles of infants drinking milk and swallow cycles of juveniles drinking milk ($P>0.8$). The EMG signals were significantly more variable in juveniles drinking milk than in juveniles eating porridge ($P<0.01$).

Discussion

Variation in intraoral transport cycles versus variation in cycles containing a swallow

The way in which we calculated variation in cycle frequency differed between the transport cycles and cycles containing a swallow; this had implications for our interpretation of the variation of these two types of cycles. The variation among transport/processing cycles was based on intervals of time that did not contain any other cycle types, i.e., it excluded cycles with swallows or cycles involving the acquisition of solid food from a bowl. This variation is a measure of the constancy or regularity of these cycles (i.e., how similar in length they were), although the oral behavior occurring during these cycles could vary. Even the apparently simple cycles of consumption of liquid by infants included two functions, i.e., getting milk out of the teat and transporting it posteriorly into the valleculae. In juveniles, the drinking cycles included both sucking milk out of the bowl and its subsequent intraoral transport (Miller 1999). In the case of porridge, more manipulation of the food is required and, for solid food, there is actual mastication. Increased variation in these cycles could be due to differences in the amount of food or liquid in the mouth, the ability of the tongue to move the food, or to the slow process of learning how to manipulate unfamiliar foods.

These transport cycles, often called the "oral phase" in the human clinical literature, are traditionally considered volitional motor responses to sensory feedback (Ross et al. 2010). Despite the fact that, in relation to movement, the terms "volitional" and "reflex" are scientifically imprecise (Prochazka et al. 2000), we will use them in this article in a particular way. We use "volitional" to mean motor activity that is dependent upon cerebral function (including transcortical reflexes) and "reflex" to mean movement dependent upon simple or polysynaptic reflex arcs within the brainstem that can produce complex movements. Certainly mastication in mammals is believed to include feed-forward control over cycles and is thought to be subject to motor learning (Miller 2002; German et al. 2004).

Our measure of variation in cycle frequency for cycles containing a swallow assessed a different aspect of variation than did our measure for transport cycles. Swallow cycles occurred relatively infrequently and instead of measuring the duration of such cycles (although that is of interest, and a subject for future analysis), we measured the frequency of occurrence of these cycles. Specifically, we measured how often they occurred during feeding, even during transport/processing cycles. Thus, variation in swallow cycle frequency did not measure variation in swallows, *per se*, but rather the variation in the time preceding a swallow which would indirectly reflect what factors were sufficient to trigger a swallow. Although the accepted view is that volume in the valleculae is the major trigger of a swallow, other results suggest that oral phase stimuli play a role (German et al. 2004). The variation in the frequency of swallow cycles was significantly less than the variation in the frequency of transport/processing cycles, suggesting that the transport/processing cycles were varied so as to assist in attaining a particular end point (e.g., bolus size or consistency) that in turn generated the sensory input necessary to elicit a swallow.

Variation in cycle frequency due to age

Variation in cycle frequency for both transport and swallow cycles was lowest in adults, as predicted, suggesting that there is a maturation of the feeding process as animals reach adulthood. One surprising result was that, for both types of cycles, infants suckling milk had lower variation in cycle frequencies than did juveniles drinking milk. Infants suckling from a bottle developed a tight intraoral seal around the artificial nipple so that the rhythmic drops in intraoral pressure, due to cyclical tongue movement, could result in highly efficient delivery of milk to the posterior oral cavity (Thexton et al. 1998). Juveniles, on the other hand, drank milk from a bowl and while the tongue still moved milk to the posterior oral cavity, a comparably tight anterior intraoral seal was not possible. Additionally, the head-down position required milk to be moved against gravity. This was in contrast to the head-up posture of suckling infants. While drinking from a bowl would appear to require more effort to transport the milk, in many muscles the amplitude of EMG activity was lower in the same individual drinking from a bowl compared to suckling from a bottle with a nipple (Thexton et al. 1998).

One concern with the interpretation of these data is that contractile properties of muscle fibers change with maturation (Vinay et al. 2000). Some of these developmental changes impact on how muscle fibers generate contractile force (Péréon et al. 1993). As such, the measurements of EMG activity that we provide here should not be taken as direct measurements of variation in contraction, the functional endpoint of kinematics. Future studies are needed to specifically address this concern.

Differences in variation in cycle frequency and EMG bursts due to consistency of food

We had a second alternative hypothesis for variation in cycle frequency and EMG signals as a function of food type. The second was that, for an animal of a given age, the increased severity of the problem that results from aspiration of solid food relative to liquid would reduce the variation in cycle frequency and EMG signal parameters for an animal swallowing solids (Thexton et al. 2007). This hypothesis was largely supported in juveniles for whom we had feeding activity on all three types of food, and for adults for whom we had two consistencies. Cycle frequencies were more variable for the intake of milk than for porridge and cycle frequencies for porridge were more variable than for solid food.

The Index of Signal Variability for swallow cycles also provided insight into neural control of muscles used in swallowing. Thexton et al. (2007) and German et al. (2009) demonstrated that, differences exist in the timing of the EMG signals between intact and decerebrate animals, during swallowing. They hypothesized that descending cerebral pathways are important regulators of the brainstem circuitry that makes swallowing possible in the decerebrate. The present results relating to signal variability indicate that descending pathways from the encephalon also play a role in maintaining some constancy of EMG activity from cycle-to-cycle.

When the level of variation of the EMG signal was measured by the Index of Signal Variability the difference in variation between swallowing milk and porridge indicates another aspect of the constancy in motor performance. Despite the fact that, for these juveniles, porridge was a novel food, and milk was not, the variation in the EMG signal of swallows was higher when swallowing milk. This suggests that the neural mechanisms protecting the airway are firmly in place prior to weaning (Crompton et al. 2008) and that variation in swallows of food with potentially more dangerous consistencies are held to a minimum.

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Supplementary Data

Supplementary data is available at *ICB* online.

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