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Babbling, Chewing, and Sucking: Oromandibular Coordination at 9 Months

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Abstract

Purpose—The ontogeny of mandibular control is important for understanding the general neurophysiologic development for speech and alimentary behaviors. Prior investigations suggest that mandibular control is organized distinctively across speech and nonspeech tasks in 15-month-olds and adults and that, with development, these extant forms of motor control primarily undergo refinement and rescaling. The present investigation was designed to evaluate whether these coordinative infrastructures for alimentary behaviors and speech are evident during the earliest period of their co-occurrence.

Method—Electromyographic (EMG) signals were obtained from the mandibular muscle groups of 15 typically developing 9-month-old children during sucking, chewing, and speech.

Results—Unlike prior investigations of 12- and 15-month-olds and adults, 9-month-olds' analyses of peak correlations among agonist and antagonist comparisons of mandibular EMG data revealed weak coupling during sucking, chewing, and babble; associated lag values for antagonist muscle groups indicated greater synchrony during alimentary behaviors and less synchrony during babble. Unlike the speech data of 15-month-olds, 9-month-olds exhibited consistent results across speech subtasks.

Conclusion—These findings were consistent with previous results in which mandibular coordination across behaviors was more variable for younger age groups, whereas the essential organization of each behavior closely reflected that seen in older infants and adults.

Keywords

speech; development; motor control; mandible; human

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An understanding of the ontogeny of mandibular motor control is critical to a more general understanding of the neurophysiologic basis for the development of speech, chewing, and sucking. There is a lack of uniformity in researchers' understanding of emerging motor control that underlies speech and early alimentary behaviors, which precludes a complete model of communication development. Although few studies have investigated mandibular muscle coordination in humans during an early period in which babble/speech coexist with alimentary behaviors (e.g., chewing from 12 to 48 months; Green et al., 1997; sucking, chewing, babble, and speech in 15-month-olds; Moore & Ruark, 1996), these investigations have supported the idea that infants and toddlers, similar to adults (Moore, 1993; Moore, Smith, & Ringel, 1988), coordinate jaw muscle activity task specifically. These consistent findings of task specificity suggest that the underlying motor organization is determined by distinct nonoverlapping task demands.

Potential Differences in Goals for Early Oromotor Behaviors

An intentional motor behavior is initiated by the translation of abstract goals into discrete motor plans (e.g., Jeannerod & Decety, 1995) that dynamically activate specialized neurons, localized networks, and larger neural ensembles (e.g., Dickinson, 1995; Greybiel, Aosaki, Flaherty, & Kimura, 1994; Katz, 1995; Pearson, 1995) to modulate and adapt the order, timing, and strength of muscular activity. This dynamic engagement of neural circuitry influences the cellular properties and synaptic interactions among these systems, such that the properties of a specific neural region can be affected by the context of its interaction with other regions of the brain, and these properties can be further influenced by task demands (Jennings, McIntosh, & Kapur, 1998; Jennings, McIntosh, Kapur, Tulving, & Houle, 1997; McIntosh, Nyberg, Bookstein, & Tulving, 1997).

Differences in mandibular muscle activation patterns may arise as distinct underlying capacities engaged to achieve the specific goals of each task (e.g., Moore, 2004; Thelen, 1991). Chewing, for example, typically requires high occlusal force during the grinding phase (i.e., lateral movement of the jaw), which occurs near the peak of jaw elevation. This occlusal force is generated by a stereotypic pattern of muscle activity: synchronous coactivation among agonist muscle groups (e.g., masseter and temporalis muscle groups) and reciprocal activation among antagonist pairs (e.g., masseter and anterior belly of the digastric; Moore et al., 1988). Speech requires far less occlusal force than chewing, with jaw movement constrained by acoustic goals (including prosodic features) and coarticulatory influences of other oral structures (McClellan & Tasko, 2003; Moore et al., 1988; Wildgruber, Ackermann, & Grodd, 2001). Greater variability in patterns of muscle activation is noted during speech, which is characterized by more frequent coactivation of antagonist muscle pairs (Moore, 1993; Moore et al., 1988). Coactivation among antagonist muscle groups during speech may enhance the mandible's intrinsic resistance to mechanical perturbations induced by other articulators (Humphrey & Reed, 1983; Shiller, Houle, & Ostry, 2005; Shiller, Laboissière, & Ostry, 2002). The increased stiffness of the mandibular system will also increase its frequency response (A. M. Smith, 1981) during speech and may provide an intrinsic equilibrium point, thereby guiding positional accuracy independent of extrinsic biomechanical factors (Bizzi, Polit, & Morasso, 1976; Perrier, Ostry, & Laboissière, 1996). Investigations of mandibular coordination (i.e., electromyographic [EMG] measures of organized mandibular muscle activity; Moore, 1993; Moore et al., 1988) support the conclusion that various neural networks at different levels of the nervous system dynamically combine (e.g., Grillner, 2003b), organizing jaw muscle activity suited to perform a given task and allowing a significant degree of plasticity for mandibular coordination across tasks.

Potential Neural Infrastructures Influencing Early Oromotor Behaviors

Neural mechanisms of pattern generation (i.e., central pattern generators [CPGs]) may influence mandibular control during sucking, chewing, and speech (e.g., Grillner, 1982, 1991; Lund, 1991). These dedicated neuronal networks dynamically interact with other neural systems across levels of the nervous system (cerebral cortex, brain stem, and spinal cord), influencing final common pathway activity across a very broad range of motor activities (Grillner, 1991, 2003a). The breadth of complexity of these neural networks spans the simple circuits that control very short latency reflexes, the more complex structures underlying patterned generation of movements such as sucking and mastication, as well as the fractionation and recombination of CPGs for more complex motor behaviors such as speech (Grillner, 1991).

Motor learning (use) and sensory feedback play a crucial role in the development (i.e., recombination) of these complex motor acts (Grillner, 1985, 1991, 2003a, 2003b). Grillner (1985) proposed innate networks, such as those underlying sucking, swallowing, and breathing, as well as latent systems, which become effective as the nervous and musculoskeletal systems mature, such as those for walking, expressing emotion, vocalizing, and hand dexterity. Development of motor control for speech may be influenced by the modulation and dynamic reassembly of these underlying neural networks, which become increasingly effective and consistent with use and refinement (e.g., Grillner, 1982, 1985). Such gradual adaptation to demand is evident even in those networks that are operational at birth, as these systems react to the immediate environment via sensory input and exhibit refinement proportional to use (e.g., Grillner, 1985).

The extent to which CPGs influence or support the emergence of a motor control structure for early babble is unknown. Lund and Kolta (2006) have hypothesized that a CPG that controls the mandible during mastication is also a primary control unit for coordination during speech. This masticatory CPG is modeled as operating under the executive control of higher centers, though it is, of course, susceptible to modulation by afferent information as well. According to this representation, differences in motor control of the mandible during chewing and speech arise from the reorganization (recombination) of subpopulations of neurons within the CPG to generate the observed range of mandibular behaviors and movement patterns.

In contrast, Jürgens argued that masticatory and articulatory rhythm generators operate at very different frequencies, with jaw movement during chewing appearing as a categorically distinct cyclic movement pattern produced, for example, at a significantly slower frequency than during vocalization (see open peer commentary in MacNeilage, 1998). Differences have also been described for the trajectory and frequency of jaw movement in humans during mastication and speech (Gibbs & Messerman, 1972). Animal studies (e.g., squirrel monkeys) by Jürgens and colleagues (e.g., Hage & Jürgens, 2006) suggest that the neural networks subserving the rhythmic pattern generation for mastication and vocalizations reside in different areas of the brain (Jürgens, 2002). These vocal behaviors entail coordination of the respiratory (usually expiratory), laryngeal (usually vocal fold adduction), and supralaryngeal vocal tract structures to modulate the aerodynamic energy required for specific calls. Empirical findings further support the idea that different neural networks along the neuraxis underlie a continuum of basic and complex levels of vocal behavior such as innate vocal reactions, imitative vocalizations, and complex vocalizations, including those that require vocal tract modulation similar to that observed for human speech (see review by Jürgens, 2002).

Early vocal behaviors in humans may be influenced by interactions among articulatory rhythm generators and neural networks underlying emerging linguistic abilities. Smith (see review by A. Smith, 2006) has described a developmental continuum for speech and language, with linguistic objectives shaping motor commands as well as motor constraints delimiting

linguistic goals. These remarkably balanced, bidirectional influences contribute to the multilayered mapping between language (linguistic units) and speech motor control (A. Smith, 2006). This principle is evident even in early preverbal vocalizations. Scheiner, Hammerschmidt, Jürgens, and Zwirner (2006) provided empirical evidence that normal hearing (NH) and hearing-impaired (HI) infants (2–7 months) use early vocalizations (i.e., cry, short cry, coo/wail, moan, whoop/squeal, hic, laugh, groan, croak, raspberry) differentially to signal positive or negative emotional states (see also Papoušek, 1989). Although these emotive (prelinguistic) sounds are presumably biologically determined—NH and HI infants produce these sounds with essentially the same acoustic structure—there are evident, distinct environmental influences. NH infants use a wider variety of vocal sequences of vocalizations, which are associated with specific acoustic changes that reliably signal respective emotions (Scheiner et al., 2006). By 3 months of age, NH infants imitate the caregiver's intonation (Papoušek, 1989) as well. Auditory feedback from the caregiver may provide reliable cues about the consequences of vocalization and probably serve as a source of learning for the NH infant (Scheiner et al., 2006). Environmental factors associated with the infant and caregiver interaction may begin to shape infant use of emotive vocalizations. This effect may underlie the emergence of pragmatics and, moreover, may be an early form of mapping between a primitive form of language and emerging motor control for speech. Other investigators have also reported that immediate feedback from the caregiver enhances the vocal productions of infants, whereas delayed feedback does not (Ramey & Ourth, 1971).

Empirical Investigations of Early Oromotor Behaviors

If early motor control for speech is significantly influenced by a masticatory pattern generator, then the coordinative organization of mandibular muscle groups for early speech might be expected to resemble the cyclic, reciprocal activation patterns among antagonist muscle groups. This reciprocal activation pattern is well documented in both animal (e.g., Lund, 1991) and human (e.g., Møller, 1966; Moore et al., 1988) models. Early mandibular motion for babble is often described as cyclic, though the relation of jaw movement trajectories to those of early appearing “ingestive cyclicities” (e.g., chewing) remains equivocal (e.g., MacNeilage, 1998). An alternative approach is that the coordinative infrastructure for speech is unique, though it may emerge under the guiding influence of such neural networks as those underlying CPG of early vocalizations (e.g., Jürgens, 1998). Of course, even as an independently developing process, speech motor control reflects the more global influences of neural maturation and development (e.g., Barlow, Finan, & Andreatta, 1997; Grillner, 1985) as well as such remarkable bidirectional influences as mapping between language and speech (e.g., A. Smith, 2006) and between the auditory and articulatory systems (e.g., Callen, Kent, Guenther, & Vorperian, 2000). Patterns of mandibular muscle activity have been used to differentiate these influences in adults (Moore, 1993; Moore et al., 1988) and toddlers (Moore & Ruark, 1996).

Similar to results measured from the EMG data of adults (Moore, 1993; Moore et al., 1988), the coordinative organization underlying mandibular movement for speech and nonspeech tasks is apparently different in 15-month-old toddlers (Moore & Ruark, 1996). This group of children exhibited significantly greater coordinative plasticity among mandibular muscles across tasks; distinct coordinative strategies for sucking, chewing, and early speech; and significant differences in EMG patterns across speech subtasks. Coupling (i.e., correlated EMG activity) among mandibular muscle pairs during sucking and chewing was significantly weaker than during speech subtasks. Thus, even at 15 months of age, observed patterns of muscle activity clearly support the notion of differential organization of speech and nonspeech tasks.

Mandibular coordination is also distinct for each of the alimentary behaviors of sucking and chewing. Ruark and Moore (1992) examined the underlying mandibular organization during suckling and sucking activity in 7 infants between the ages of 1 and 11 months and in seven

15-month-olds (Moore & Ruark, 1996). Infants and 15-month-olds exhibited similar muscle activation patterns during chewing, suckling, and sucking; homologous muscle groups (e.g., left and right masseter) exhibited a significant degree of coupling (i.e., highly correlated activity within muscle pairs) and synchrony. The primary difference between chewing and sucking and suckling was observed in the masseter antagonist comparisons (e.g., activity of left-masseter activity with respect to that of anterior belly of the digastric [ABD]). During suckling and sucking, activity of the masseter with its antagonists was highly synchronous, whereas during chewing, these antagonists exhibited greater asynchrony in adults (Moore, 1993; Moore et al., 1988), infants, and young children (12–48 months; Green et al., 1997; 15 months; Moore & Ruark, 1996). These distinctions in the organization of mandibular motor control may reflect varying interarticulatory constraints among oral structures (e.g., tongue) arising from widely varying task demands. Neural networks may organize differently for controlling motor patterns distinctively across oromandibular behaviors. Empirical evidence from rats reveals distinct neural representations for suckling and early chewing at birth (Iriki, Nozaki, & Nakamura, 1988; Westneat & Hall, 1992), and perhaps most significantly that the coordinative infrastructure for suckling is not a precursor for the emergence of later feeding behaviors (Hall & Williams, 1983).

Previous investigations have further demonstrated that maturation of sucking, chewing, and early speech in infants and toddlers is characterized primarily by the refinement and rescaling of existing mandibular coordinative patterns rather than by newly emergent structures or generalization of earlier established skills (Green et al., 1997; Moore & Ruark, 1996; Ruark & Moore, 1992). For example, 12-month-olds' mandibular coordination for chewing (Green et al., 1997) was similar to that observed in adults (Moore, 1993; Moore et al., 1988). Chewing by these infants, like the adults, was characterized by reciprocal activation among antagonistic muscles, though patterns of activity were significantly more variable. The coordinative organization of chewing appeared to become more efficient and stable from 12 to 48 months of age (Green et al., 1997), as measured by stronger (increased) coupling of activity across jaw elevator muscles, greater asynchrony among antagonistic muscles, and shorter EMG burst durations for all muscle groups over this developmental period. A distinct pattern of reciprocal activation among antagonists was well established by the age of 48 months (Green et al., 1997). No significant difference was noted in the rate of chewing, but the variability in rate decreased significantly from 12 to 48 months (Green et al., 1997).

Like chewing, mandibular muscle coordination for syllable and true-word production in 15-month-olds (Moore & Ruark, 1996) resembles that of adult speech (Moore, 1993; Moore et al., 1988), the stability of these coordinative patterns being somewhat more variable in the toddler. Overall, 15-month-olds exhibited significantly weaker coupling (i.e., lower average peak cross-correlation coefficients) across muscle group comparisons than adults (Moore, 1993; Moore & Ruark, 1996; Moore et al., 1988). At 15 months of age, true-word productions composed of reduplicative or variegated bisyllables were produced with greater coupling across muscle groups than reduplicative and variegated babble productions (Moore & Ruark, 1996). Possibly, multilayered mapping between language and motor control of speech (e.g., A. Smith, 2006) becomes more stable as the toddler begins to produce a larger lexicon of true words. Together, these observations of EMG for chewing and speech support the notion that by 12–15 months of age, distinct motor programs underlie mandibular coordination for specific speech and nonspeech tasks, with maturation characterized by the refinement of existing coordinative infrastructures.

Empirical Questions Addressed by This Investigation

The question remains whether there is an identifiable coordinative organization across mandibular muscle groups within a given task that is comparable to that reported in prior studies

of adults (Moore, 1993; Moore et al., 1988) and toddlers (Green et al., 1997; Moore & Ruark, 1996) and whether this organization exhibits a level of task specificity during the earliest period of co-occurrence for sucking, chewing, and babble. The refinement that characterizes motor development of these behaviors may be derived from earlier forms that are so variable (i.e., low correlation across muscle group activity) that within-task and between-task differences are not discernable. More importantly, later appearing task differences may suggest differential rates of development, which might be detected in differences in coordinative stability for early emerging forms. The present investigation was designed to evaluate these task-specific differences during this very early period of task emergence through three experimental questions addressing (a) whether the degree of coupling and asynchrony (i.e., relative timing of EMG activity) is different among mandibular muscle group comparisons within the behaviors of sucking, chewing, and babble; (b) whether these measures among muscle group comparisons are different across behaviors; and (c) whether these measures among muscle group comparisons for given behaviors are different across age groups.

Within chewing and babble, coupling among homologous muscle groups would be anticipated to be higher than among other synergist pairs (i.e., ipsilateral and contralateral), and coupling among synergist muscle groups would be expected to be higher than antagonist comparisons, which have been measured in adults (chewing and speech; Moore, 1993; Moore et al., 1988) and toddlers (chewing; Green et al., 1997; chewing and babble/speech; Moore & Ruark, 1996), with slight differences in organization noted among masseter antagonist comparisons during sucking (Moore & Ruark, 1996). Between behavior, comparisons of coupling and timing (i.e., asynchrony) among muscle groups might reasonably be predicted to be different for babble and alimentary behaviors (Moore & Ruark, 1996); however, if coupling (i.e., correlated muscle activity) is observed to be weak (i.e., low coefficients) among mandibular muscle groups, then the still-forming coordinative infrastructure for mandibular control may be understood as remaining unspecified during this period of early development of sucking, chewing, and speech. If the degree of coupling (i.e., the predictability of activity between muscle groups) among specified muscle group comparisons significantly increases across age groups, then coordinative stability would appear to be emerging for the given task, such as noted for chewing (Green et al., 1997). This finding would be expected to also be accompanied by adjustments in the relative timing (i.e., asynchrony) in activity among muscle group comparisons.

Method

Participants

Fifteen 9-month-old infants (6 boys, 9 girls) were observed during naturally occurring activities that involved oromandibular movement. These children participated in this experiment as part of an ongoing longitudinal study of the development of oromandibular coordinative organization during sucking, chewing, and babble. According to parental report, each participant had normal achievement of gross motor, fine motor, cognitive, speech (babble), and language milestones. Each infant passed otoscopic and tympanometric screening to reduce the chance of including children with active middle ear pathology.

Experimental Protocol—After familiarization with the researchers and setting, the infant was seated and secured in a high chair with a leg strap and sliding tray. The child's caregiver and an experimenter were seated next to the child throughout data collection. The experimenter monitored the child's behavior and provided an online commentary of the subject's activities; foods consumed; verbal marks of the child's onset of sucking, chewing, and swallowing; and the occurrence of extraneous movements. The child's interest dictated the order in which the target behaviors of sucking, chewing, and babble were observed. Sucking behavior was

measured during breast- and bottle-feeding. Food items for chewing were provided by the caregiver and were representative of the child's typical diet. These items included fresh fruits and vegetables, bread, rice cakes, cookies, cereal, and crackers. A longitudinal investigation of chewing development in children from 12 to 48 months by Green and colleagues (1997) included 4 children who participated in this present study. An unfortunate consequence of working with 9-month-old infants is that it was rarely possible to identify the working side of the mandible during chewing. Therefore, the working versus nonworking side of the mandible was not identified in this investigation.

Babble tokens produced by the 9-month-olds were further classified into subtypes. This distinction was motivated by earlier results in 15-month-old children (Moore & Ruark, 1996) that demonstrated weaker coupling for reduplicative babble compared with later emerging speech behaviors. The present investigation compared mandibular organization during reduplicative and variegated babble with other speech types. Five investigators independently judged the corpus-of-speech behaviors, classifying each token into one of three mutually exclusive categories: *reduplicative babble*, which included sequential repetitions of a single syllable; *variegated babble*, which included clear changes in the vocalic and/or consonantal portion across syllables; and *other speech types*, which were utterances that were clearly differentiable from reduplicative and variegated babble. A babble sample was classified into one of the three categories only if complete agreement was independently reached among the five investigators. A babble sample unreliably classified into one of the three categories was labeled *unidentifiable*.

Electromyography and Data Recording—EMG and audio data were recorded continuously for about 45 min during an experimental session. Targeted mandibular muscles included the primary muscles of mastication: (a) right masseter, (b) left masseter, (c) right temporalis, (d) left temporalis, and (e) ABD. Biomechanically, the masseter and temporalis muscle groups are consistent with elevating the mandible, whereas the ABD muscle group depresses the jaw. When obtaining EMG recordings from 9-month-olds, a significant challenge posed was appropriate placement of the electrodes and maintenance of secure contact. EMG activity for masseter was recorded over the main mass of the muscle where masseter is superficial to other muscles and activity is most easily recorded. Similarly, the EMG activity from the temporalis was probably well isolated, as this large muscle is quite separate and distant from muscles whose activity is likely to contaminate that of the target (i.e., temporalis) muscle. Targeting the ABD, a primary jaw depressor, was somewhat more challenging, as this muscle is relatively small and is proximal to several larger muscles, including the mylohyoid and platysma. These concerns were mitigated somewhat by the fact that the ABD is the most superficial muscle at the EMG recording sites as well as by recognizing that activity in muscles proximal to the digastric is biomechanically consistent with mandibular depression during sucking, chewing, and babble (speech). Thus, although the ABD was the targeted muscle, other suprahyoid muscles that might be active for mandibular depression were likely included in these EMG recordings.

EMG recordings of mandibular muscle activity were obtained bilaterally using miniature surface Ag/AgCl electrodes (In Vivo Metric, Healdsburg, CA) placed over the main masses of the right- and left-masseter and temporalis muscles, and recordings of ABD were recorded bilaterally using a single electrode pair. Placement of masseter and temporalis electrodes was based on palpation of anatomical landmarks. Electrodes for the bilateral masseter muscles were aligned vertically over the main mass of each muscle superior to the angle of the mandible, and electrodes for temporalis muscles were aligned obliquely just superior to the zygomatic arch. Electrodes within each pair were spaced approximately 0.5 cm apart and aligned parallel to the orientation of the muscle fibers. Obtaining EMG recordings of the targeted ABD required an approach that was different from the procedures used with masseter and temporalis sites.

The digastric recording site was immediately posterior to the mental symphysis. The small size of this muscle and, in infants, the substantial amount of fatty tissue overlying the digastric more posterior to the chin precluded unilateral recordings of the ABD. Therefore, using a single electrode pair, an electrode was placed over each belly of the right and left ABD at an interelectrode distance of approximately 0.5 cm. A reference electrode was placed approximately 2 cm superior to the nasion. These EMG signals were amplified (Grass P511; gain ranged from 10,000 to 100,000; bandpass: 3–3000 Hz) and recorded with the use of a 14-channel instrumentation frequency-modulated recorder frequency response: DC-1250 Hz; signal-to-noise (S/N) ratio > 50 dB (Teac XR-510).

A foremost concern of this study and in the prior series of investigations targeting this longitudinal data set (Green et al., 1997; Moore & Ruark, 1996) has been potential crosstalk between surface EMG recordings. This concern was addressed by (a) monitoring intra- and intermuscular placement of the surface electrodes; (b) explicitly quantifying crosstalk in the EMG recording from the 15-month-old's data set, which followed the same data-acquiring protocol as this investigation; and (c) observing the overlap of EMG activity between muscle pairs from the prior longitudinal study of chewing development. The relatively large distance between electrode pairs (i.e., compared with the distance within electrode pairs) reduced the risk of volume conduction effects. In addition, Moore and Ruark (1996) have quantified crosstalk in a data set from 15-month-olds using analysis of coherence, finding that these data were free of detectable levels of mutual interference. Finally, Green and colleagues (1997) studied chewing development in 4 children across a longitudinal data set that included 13 sessions per child from 12 to 48 months of age. Their finding of asynchronous EMG onsets and offsets supported their claim of successful isolation of activity in each of the target muscles.

Postprocessing of Event-Related Data

Preliminary inclusion criteria: Identification of acceptable intervals of EMG activity associated with sucking, chewing, and babble relied on the experimenter audio description provided by two of the investigators as well as visual inspection of the signals. Nonnutritive sucking and chewing events were excluded from the data set. The EMG signals obtained from the 9-month-olds were consistent with observations reported in prior investigations of very young children; burst duration and activation patterns were more variable than those noted for 48-month-olds and adults (Green et al., 1997; Moore, 1993; Moore & Ruark, 1996; Moore et al., 1988). Although the present analytic procedures were designed explicitly for EMG with relatively high levels of noise (e.g., biologic noise, poor S/N ratio), data inclusion was conservatively controlled to exclude artifact and extremely low levels of task-related EMG modulation. EMG signals included in this investigation were free of movement artifact, exhibited line noise that was less than 10% of the spectral energy between 1 and 200 Hz, and included task-related modulation of 3 dB or greater. *Movement artifact* was defined as a spurious signal not associated with muscle activity, such as a low-frequency modulation of the EMG signal creating a DC offset from baseline.

Parsing and digitization of data: Intervals of EMG activity related to sucking, chewing, and babble were digitally parsed from the continuous 45-min recording of each participant's session using a commercially available hardware/software system (Windaq, Dataq Instruments, Akron, OH; sample rate 1,000 samples/s). Online commentary from the experimenters, characteristics of EMG activity associated with the target behaviors (e.g., Møller, 1966; Moore et al., 1988), and audio from the infant were monitored for identifying sucking, chewing, and babble behaviors. The onset of sucking and chewing could be identified as exhibiting the lowest level of muscle activity across all five EMG channels prior to the initial burst of EMG usually across jaw-elevating muscle groups (i.e., bilateral masseter and temporalis agonists), which was followed by subsequent bursts of phasic activity between jaw-elevating and -depressing (i.e.,

ABD) muscle groups prior to the swallow. The terminal boundary of the sucking and chewing event included the last phasic burst of sequential mandibular EMG activity before the initiation of the swallow. The swallow event was identified in the commentary as well as in the cessation of phasic EMG activity prior to the swallow. The initial and final boundary of EMG-associated babble corresponded to the onset and offset of the audio signal. An EMG babble segment was judged as continuous until the utterance (i.e., audio channel) terminated or was interrupted for more than 300 ms. After parsing the data sample, continuous EMG signals associated with sucking and chewing for each participant were saved in cumulative data files (i.e., sections of parsed data were appended as a continuous series); those associated with babble were saved separately in individual data files. The babble EMG samples were saved separately because these tokens were later categorized into different types of babble. The sucking and chewing EMG samples were composed as a single event—either sucking or chewing. The audio from each participant's babble files was also saved to a cumulative file that was used for subsequent classification (perceptual) of the babble tokens.

Data Analysis

Cross-correlation: Continuous and cycle-by-cycle analysis: Following digitization of these data, several analyses of each token were computed using custom algorithms designed for MATLAB (Version. 5.0; The Mathworks, Inc., Natick, MA). The computer-assisted analysis read each data file, providing the experimenter with successive measurement windows, each being no more than 10 s in length and consisting of five EMG channels and one audio channel. This process yielded cumulative records of sucking and chewing, incorporating segments of approximately 9-s durations each. The babble records were more variable in duration, ranging from approximately 1 to 9 s as the experimenter selected only that portion of the EMG record that corresponded to audible babble. Following parsing, each EMG channel of a selected token was subjected to preliminary inclusionary analyses.

As shown in Figure 1, signals meeting the inclusion criteria were full-wave rectified and digitally low-pass filtered (8-pole Butterworth, $f_c = 30$ Hz; Krohn-Hite Corp., Brockton, MA) to generate an amplitude envelope showing the burst pattern for each EMG channel. Cross-correlation functions were computed in a pairwise fashion for these rectified and filtered signals, yielding 10 possible muscle pairings such as agonist comparisons of right masseter with left temporalis or antagonist comparisons of right masseter with ABD. The peak coefficient of the cross-correlation provided a quantitative measure of coupling for each pair of EMG signals; the lag associated with that peak provided an indication of the asynchrony of related activity within these pairs. The measure of coupling quantified the degree of organized activity across muscle pairs, whereas the measure of asynchrony provides a relative measure of timing. Across all observed muscle pairs, calculation of the strength of activation coupling and the relative timing of activation yielded 10 possible coefficients (coupling) and corresponding lag (asynchrony) values for each token.

This analytic approach was designed to replicate prior investigations of these behaviors at older ages (i.e., 12 and 15 months). The present investigation extended earlier studies by incorporating a within-subject comparison of the muscle activation coupling in these 9-month-olds during sucking, chewing, and babble.

In adults, Moore (1993) reported that the cyclic EMG signals associated with chewing were characterized as being tightly coupled among homologous pairs (e.g., average peak correlation coefficient = .66), whereas during speech, coupling was significantly weaker (e.g., average peak correlation coefficient = .43). The surface EMG signals of very young children, however, exhibited lower absolute amplitude (Green et al., 1997; Moore & Ruark, 1996) and a poor S/N ratio. This potential confound was evident when the present 9-month-olds' EMG records were compared with those of 12-month-olds (Green et al., 1997). Accordingly, a cycle-by-

cycle approach that was less susceptible to long-term changes in the signal (e.g., period drift) was adopted for the sucking and chewing data. Cross-correlation functions were computed only for successive cycles of these cyclic records. Coefficients computed over successive cycles of a single sequence were averaged to provide a single coefficient value for that event. This cycle-by-cycle analysis was not performed on the EMG data from speech events because these tokens were not cyclic, as expected.

Rate analysis: Age-related changes measured in the asynchrony of activity among muscle groups might be related to changes in the rate of sucking or chewing (e.g., Green et al., 1997). Sucking and chewing rates were computed from the EMG records. The procedures described for the cross-correlation function were used in this analysis. The user had a window of at least 10 s from which to parse an interval of EMG data meeting the inclusionary criteria. Each channel of the user-selected segment of EMG was full-wave rectified, low-pass filtered at 30 Hz, and its autocorrelation function was computed. Fast Fourier transformation functions were computed for each autocorrelation function, which yielded the spectral density for each channel. Peak spectral energy within the physiologic range of mandibular movement for chewing was identified, and the corresponding frequency was used as an estimate of rate of mandibular elevation/depression for that channel. The absence of an identifiable peak in the power spectrum for a particular channel led to the rejection of that channel from the rate analysis. Rate values across channels were generally equivalent. When there was a disparity in rate for a given channel, the rate for that channel was usually identified as the mode of the rates calculated from each of the remaining EMG channels, as these values were usually equivalent. In a very few instances for which rate value was slightly different across channels, the overall rate was estimated as the mean rate across all channels. Rate means and standard deviations for sucking and chewing were calculated as the mean and standard deviation across participants' means.

Measurement Reliability—The appended data records obtained during sucking by 2 participants and during chewing by 2 other subjects were randomly selected for analysis of reliability. Two experimenters reanalyzed these 4 participants' appended data files using the continuous cycle and cycle-by-cycle analyses for obtaining the peak correlation coefficient and lag values that occurred during sucking and chewing. Forty-four multiple-cycle and 513 single-cycle tokens were reanalyzed. For all multiple-cycle and single-cycle measures from each participant, the absolute difference between the average peak coefficients across all muscle pairs obtained by two experimenters never exceeded .05, and lag values were never greater than 24 ms. These differences were acceptable for the present analysis. Measurement reliability was not performed on the speech data because these tokens were saved as individual files. Parsing and analysis of speech data required minimal user input, as analyses included an entire token for each computation (i.e., there was no user intervention during analysis).

Statistical Treatment—Coupling strength between muscle pairs was quantified by the peak cross-correlation coefficients, and asynchrony of muscle activation was measured as the lags associated with these coefficients. All peak coefficients were transformed to Fisher's Z values to normalize the distributions of these data permitting statistical comparisons within and across subjects. Within-subject averages were computed for each task. These mean peak coefficients across tasks are presented in Figure 2. The average coefficients and associated lag values were computed from each subject's data corpus for bilateral masseter, bilateral temporalis, ipsilateral synergists (e.g., right masseter with right temporalis), contralateral synergists (e.g., left masseter with right temporalis), masseter antagonists (e.g., right masseter with ABD), and temporalis antagonists (e.g., left temporalis with ABD). These six muscle groups were defined by innervation and biomechanical relations. The 9-month-old chewing data were compared with prior results obtained by Green et al. (1997); these infants' sucking and babble data were

similarly compared with those obtained by Moore and Ruark (1996). A one-way repeated measures analysis of variance (ANOVA) was used to evaluate statistical differences within the 9-month-olds' data, and a two-way analysis of variance was used for comparing across age groups. Tukey's honestly significant difference (HSD) test was used for post hoc analysis of differences.

Results

The Data Set

The EMG data for sucking were generated by 8 subjects who produced about 920 s (~1,200 cycles) of activity; from these EMG data, 701 coefficients and lags were computed using continuous analysis, and 8,936 coefficients and lags were computed using cycle-by-cycle measures. The chewing data were generated by 15 subjects, producing about 1,560 s (1,136 cycles) of chewing, yielding 156 coefficients and lags for the continuous analysis and 8,230 coefficients and lags for the cycle-by-cycle measures. Fifteen subjects contributed to the main corpus of babble data, producing 289 tokens, ranging in length from .794 to 6.074 s; the continuous analysis of these tokens yielded 1,761 coefficients and lags. From these samples of babble, 8 subjects produced 33 tokens of reduplicative babble (260 coefficients and lags), 7 subjects produced 18 tokens of variegated babble (127 coefficients and lags), and all 15 subjects produced 204 tokens of other speech types (1,164 coefficients and lags). The length of the EMG data associated with reduplicative babble averaged 2,237 ms ($SD = 283$ ms), variegated productions averaged 2,820 ms ($SD = 1,367$ ms), and other speech tokens averaged 2,258 ms ($SD = 1,100$ ms). Thirty-four speech tokens were labeled as unidentifiable.

Rate of Mandibular Movement for Alimentary Behaviors

We calculated sucking rates for the subjects in this study from a total of 67 sucking events. These values varied between 1.3 and 2.07 Hz across subjects and yielded a mean sucking rate of 1.73 Hz ($SD = 0.24$ Hz). This value is in good agreement with the data of McGowan, Marsh, Fowler, Levy, and Stallings (1991), who reported mean intersuck intervals of .57 s (1.75 Hz) in their 9-month-old subjects during nutritive sucking. A total of 139 chewing events were used in the calculation of chewing rate. The rate of mandibular oscillations during chewing ranged between 1.23 and 1.99 Hz across subjects. The mean chewing rate was 1.56 Hz ($SD = .22$ Hz). These values are comparable to those of the 12- to 48-month-olds reported by Green and colleagues (1997), which were between 0.88 and 2.11 Hz across subjects and ages. Similar to the earlier investigation by Green and colleagues (1997), infants in the present investigation chewed a variety of food consistencies that were inclusive of each child's normal diet. Other investigators have reported negligible differences in chewing rates with harder and softer foods (Gisel, 1991; Schwaab, Niman, & Gisel, 1986). Schwaab and colleagues (1986) did report significant differences in chewing rate for pureed consistencies.

Comparisons of Coupling and Asynchrony of Mandibular Muscle Activation

Comparisons across babble subtasks: 9-month-olds—We computed repeated measures one-way analysis of variance for each of the six muscle comparisons across the babble subtasks: reduplicative babble and variegated babble; reduplicative babble and other speech types; and variegated babble and other speech types. Statistical differences among these subtasks for both coupling and asynchrony within each of the six muscle comparisons were not significant. Accordingly, all babble subtasks were collapsed into a single task category.

Comparisons within behavior: 9-month-olds—We computed within-behavior statistics between similar muscle group comparisons of the 9-month-olds' EMG data during sucking, chewing, and babble. Repeated measures one-way ANOVA revealed significant differences in coupling between muscle groups during sucking, $F(5, 30) = 4.37, p = .004$;

chewing, $F(5, 70) = 18.589, p < .001$; and babble, $F(5, 60) = 13.644, p < .001$, and the relationship between these muscle groups varied across behaviors. We used Tukey's HSD test for all post hoc pairwise multiple comparisons ($p < .05$). The multiple comparisons with significant differences are presented in Figure 2 under the heading "Comparisons within Behavior: 9-month-olds." During sucking, the bilateral masseter muscle group exhibited greater coupling than the ipsilateral and contralateral agonists, and the temporalis antagonist group. During chewing, the agonist comparisons (i.e., jaw elevators) were more tightly coupled than either of the antagonist groups. More within-task variability among muscle pair comparisons was noted during babble, in that bilateral masseter coupling was greater than that of ipsilateral and contralateral agonists (jaw elevators), and both antagonist groups; bilateral temporalis and ipsilateral agonists coupling was greater than that of either antagonist group, and contralateral agonists coupling was greater than that of temporalis antagonists. We noted significant differences in synchrony between the muscle groups during sucking, $F(5, 30) = 6.966, p < .001$; chewing, $F(5, 70) = 46.36, p < .001$; and babble, $F(5, 60) = 19.479, p < .001$. During sucking, the activity of the bilateral masseter muscle group was more synchronous than that of the ipsilateral and contralateral agonists and the temporalis antagonists; the synchrony of the bilateral temporalis agonist and masseter antagonist muscle groups was greater than for the temporalis antagonists. During chewing, the synchrony of activity of the agonist muscle groups was greater than for the antagonists. Among agonist comparisons during chewing, the bilateral masseter group exhibited greater synchrony than the contralateral pairs, and among antagonists, the masseter homologous pair showed greater synchrony than the temporalis pair. During babbling, agonist comparisons (jaw elevators) yielded greater indications of synchrony than antagonists.

Comparisons across behaviors: 9-month-olds—At 9 months, we obtained between-behavior differences for sucking and chewing and for sucking and babble. Statistical comparisons of the babble data and the alimentary data were based on the cycle-by-cycle analyses. A repeated measures one-way ANOVA was computed separately for each of the six muscle pair comparisons across these behaviors, and we used Tukey's HSD test for all post hoc multiple comparisons ($p < .05$) to determine which behaviors were significantly different. These post hoc comparisons with significant differences are presented in Figure 2 under the heading "Comparisons across Behaviors: 9-month-olds." Among the jaw elevator pairs, bilateral temporalis, $F(2, 12) = 5.47, p = .02$, as well as ipsilateral, $F(2, 14) = 13.03, p < .001$, and contralateral, $F(2, 14) = 7.47, p = .006$, agonists were significantly more coupled during chewing and babble than during sucking. Among the antagonists, the masseter with ABD comparisons, $F(2, 12) = 5.71, p = .018$, revealed tighter coupling during sucking than babble. None of the remaining comparisons of coupling was statistically significant. Synchrony of agonist muscle pairs was not significantly different across the three behaviors, although masseter, $F(2, 12) = 14.58, p < .001$, and temporalis, $F(2, 12) = 12.03, p = .001$, antagonist muscle pairs were more synchronous during sucking than during chewing and babble.

Comparisons across age—We used a two-way ANOVA to measure the developmental continua of coupling and asynchrony for agonist and antagonist muscle groups during sucking, chewing, and babble. Age-related changes for alimentary and babble behaviors were significantly different. These significant main effects for age are presented in Figure 2 as "Comparisons across Age." Comparisons of sucking by children at 9 and 15 months (Moore & Ruark, 1996) indicated that the degree of coupling increased with age for both agonist and antagonist muscle groups, $F(1, 40) = 21.705, p < .001$. The only changes in timing (asynchrony) occurred among antagonists, $F(1, 20) = 4.92, p = .038$, with these muscle groups becoming more asynchronous with age. A significant main effect for age is noted from 9 to 12 months (Green et al., 1997) for coupling during chewing; agonist, $F(1, 52) = 8.931, p = .004$, and antagonist, $F(1, 26) = 22.987, p < .001$, muscle groups were shown to increase their coupling.

Significant changes in timing (asynchrony) for chewing occurred by 12 months of age, $F(1, 26) = 11.206, p = .002$, during which the antagonist muscle groups became less synchronous.

The 9-month-olds' babble was compared with each of the 15-month-olds' babble/speech subtasks, which included reduplicative and variegated babble and consonant–vowel (CV), consonant–vowel–consonant (CVC), reduplicative CVCV, and variegated CVCV word forms. When the 9-month-olds' babble was compared with the 15-month-olds' reduplicative babble, only the agonist muscle groups significantly increased in coupling, $F(1, 56) = 10.809, p = .002$. This comparison was unique in that the antagonist muscle group comparisons did not reach significance. A significant increase in coupling was noted for both agonist and antagonist comparisons between the 9-month-olds' babble and the 15-month-olds' variegated babble, $F(1, 56) = 9.706, p = .003$; $F(1, 28) = 6.868, p = .014$, and word forms, which included CV, $F(1, 56) = 15.799, p < .001$; $F(1, 28) = 28.366, p < .001$; CVC, $F(1, 52) = 29.381, p < .001$; $F(1, 26) = 35.319, p < .001$; reduplicative CVCV, $F(1, 52) = 22.153, p < .001$; $F(1, 26) = 21.361, p < .001$; and variegated CVCV, $F(1, 40) = 5.412, p = .025$; $F(1, 20) = 4.60, p = .044$. Changes in timing for the speech tasks were unlike those noted for the alimentary comparisons: Between 9 and 15 months, significant changes in timing for speech/babble were characterized by greater synchrony, whereas the alimentary behaviors displayed decreasing synchrony for antagonist comparisons. Compared with the 9-month-olds' babble, the agonist muscle groups of the 15-month-olds' CVC productions, $F(1, 52) = 6.082, p = .017$, and the antagonist muscle groups of their variegated babble, $F(1, 28) = 4.249, p = .049$; CV, $F(1, 28) = 18.596, p < .001$; and CVC, $F(1, 26) = 4.898, p = .036$, word forms each exhibited greater synchrony.

Discussion

Grillner and Wallén (2004, p. 3) proposed that a “general motor infrastructure” is available for generating diverse motor patterns at birth, and that “most, if not all” of these motor patterns are voluntarily recruited to serve the needs of the organism and are modified substantially through maturation and learning. The present set of mandibular EMG data is generally supportive of this proposal. The underlying coordinative organization for mandibular movement in 9-month-olds was significantly less specified than that noted in 12- to 48-month-olds (Green et al., 1997; Moore & Ruark, 1996) and adults (Moore, 1993; Moore et al., 1988). Even for the cyclic behaviors of sucking and chewing, the degree of coupling for muscle groups was significantly lower for both agonists and antagonists. This overall finding was consistent with previous results in which mandibular coordination was less organized for younger age groups.

Comparisons Within Behavior

Although the motor infrastructure for mandibular control was less specified (i.e., significantly weaker coupling) at 9 months of age, an identifiable coordinative organization, as reported in prior investigations, was observable for sucking, chewing, and babble. This organized coupling among muscle group comparisons suggests that basic motor patterns are in place early in development for sucking, chewing, and babble and that underlying neural networks undergo modification by activity-dependent mechanisms and sensory experience (e.g., Grillner, 2003b). For sucking, cycle-by-cycle comparisons of coupling revealed that the 9-month-olds exhibited an organizational pattern that was categorically similar to that noted for older toddlers (Moore & Ruark, 1996; Ruark & Moore, 1992). As in the older toddlers, homologous masseter activity during sucking exhibited greater coupling than that of ipsilateral and contralateral synergists as well as temporalis antagonists. Moreover, the homologous masseter activity exhibited greater synchrony than the ipsilateral and contralateral synergists as well as the temporalis antagonists.

The categorical similarity of the coordinative organizations of babbling and chewing at 9 months of age was similar to the within-behavior comparisons reported for 15-month-olds and adults (Green et al., 1997; Moore, 1993; Moore et al., 1988; Moore & Ruark, 1996). The degree of coupling and synchrony among jaw elevators was greater than that noted among antagonists. Nine-month-olds exhibited a coordinative pattern of babble that was similar to babble/true words at 15 months (Moore & Ruark, 1996) and speech for adults (Moore, 1993; Moore et al., 1988). During chewing, the pattern of coupling for 9-month-olds was similar to that noted in older infants, children, and adults (Green et al., 1997; Moore, 1993; Moore & Ruark, 1996; Moore et al., 1988).

Comparisons Across Behaviors

The degree of coupling observed among mandibular muscles in 9-month-olds was generally weaker than that observed previously in older age groups, such that findings of differences within behaviors must be carefully considered in this overall framework. Comparisons within and across behaviors suggest that basic, identifiably distinct motor patterns are in place for sucking, chewing, and babble early on but that these coordinative infrastructures are comparatively poorly organized. These comparisons are consistent with, and extend to, earlier ages; according to findings by Moore and Ruark (1996), the mandibular coordination of early emerging alimentary behaviors (e.g., sucking and chewing) is not demonstrably more developed (e.g., less variable, more rigidly assembled) than later emerging, more complex behaviors (e.g., speech subtasks). These data do not support models suggesting that the coordinative organization of babble emerges from earlier established coordinative infrastructures for behaviors, such as chewing or sucking (MacNeilage, 1998); rather, the coordinative infrastructure for sucking, chewing, and babble appear to undergo a protracted period of refinement and rescaling, essentially free of quantal changes in existing coordinative organization.

Comparisons Across Age

Refinement and rescaling of existing coordinative patterns were evident in the changes observed for each of the behaviors studied. The coordinative organization of the mandible became significantly more stable and predictable from 9 months to the later age groups. Motor patterns for sucking, chewing, and babble exhibited basic infrastructures that were relatively poorly defined at 9 months of age. The present findings, considered in the context of earlier studies, suggest that these activation patterns adapt, through continuing use and experience, to the increasing linguistic, anatomical, physiological, and communicative demands imposed on the oral motor control systems (e.g., Grillner, 1985). Between 9 and 15 months (Moore & Ruark, 1996), coupling increased for both agonist and antagonist muscle groups for sucking, and between 9 and 12 months (Green et al., 1997), coupling increased among all muscle groups for chewing. This finding of a developmental continuum supports the further suggestion that mandibular coordination emerges from distinct motor patterns that are initially poorly organized and are gradually refined with development. This suggestion is critically supported by intracellular recordings from rats, indicating that suckling and later feeding skills emerge from distinct cortical networks (Iriki et al., 1988). The coordinative infrastructure for suckling is not a prerequisite for the emergence of later feeding behaviors (Hall & Williams, 1983); rather, these related, but distinct, motor patterns emerge in parallel.

Like chewing and other alimentary functions, motor control for babble becomes more tightly coupled from 9 to 15 months, as most comparisons of coordinative stability revealed an increase across this period (Moore & Ruark, 1996), the exception being a decrease in coupling for antagonist pairs during reduplicative babble. This finding of intertask differences coincident with parallel developmental changes suggests that the neural infrastructures supporting the motor development of sucking, chewing, and early speech are each continuously influenced

by maturation, development, and use. It seems likely, even necessary, that maturation of these distinct oral motor behaviors must entail the development of sensorimotor interactions that differ categorically across behaviors. Confirmatory empirical evidence is accumulating in this regard. For example, models of speech development uniformly invoke an increasing role for auditory (Guenther, 2006) and linguistic (Callen et al., 2000; A. Smith, 2006) feedback, whereas development of sucking and mastication undoubtedly rely on emerging changes in dentition (via the periodontal ligament) and the perioral sensorium (Barlow et al., 1997; Finan & Barlow, 1998; Herring, 1985; Huang, Zhang, & Herring, 1994). Even across speech behaviors, gross coordinative changes may be taken to signal developmental stages. Moore and Ruark (1996) reported significantly stronger coupling among mandibular muscles in 15-month-olds for multisyllabic speech (true words) compared with multisyllabic babble. Thus, babble may not emerge as the serendipitous consequence of jaw movement coincident with vocalization (cf. frame/content theory; MacNeilage, 1998; silent mandibular oscillations; Meier, McGarvin, Zakia, & Willerman, 1997); but rather, emergent vocalizations in humans, like other species, appear to rely on distinct, specialized neural infrastructures (e.g., Grillner, 1985; Jürgens, 2002) adapted to signal information regarding basic emotional states (e.g., Scheiner et al., 2006).

As the organization of mandibular coordination is refined across age groups, divergence in the relative timing (asynchrony) of activity among muscle groups also becomes apparent for alimentary behaviors and speech, providing another indicator of task difference in these emerging motor patterns. Consistent with the adult pattern (e.g., Moore et al., 1988), relative timing among antagonist pairs revealed decreased synchrony for chewing (at 12 months; Green et al., 1997) and greater synchrony for babble/speech (at 15 months; Moore & Ruark, 1996). Decreased synchrony among antagonist pairs was also noted for sucking from 9 to 15 months (Moore & Ruark, 1996). These adjustments in relative timing across age groups and across behaviors also support the parallel development of coordinative infrastructures for sucking, chewing, and babble (speech). Finally, the present findings suggest that these changes in relative timing among mandibular muscle groups were not due simply to changes in the rate of EMG activity.

Conclusion

The present findings support prior conclusions that mandibular motor control is weakly prescribed in younger children (e.g., 9-month-olds), although the internal organization of this control does exhibit gross, but identifiable, similarities to the task-specific patterns seen in older infants and adults. Specifically, the organization of mandibular motor control in 9-month-olds for sucking, chewing, and babble resembles that seen in older toddlers (Green et al., 1997; Moore & Ruark, 1996), and the patterns associated with chewing and babble at 9 months appear to be emerging forms of those seen in the chewing and speech in adults (Moore, 1993; Moore et al., 1988). The essential properties of the coordinative organization of these behaviors appear to be established very early in development, even though they are rather poorly specified at first.

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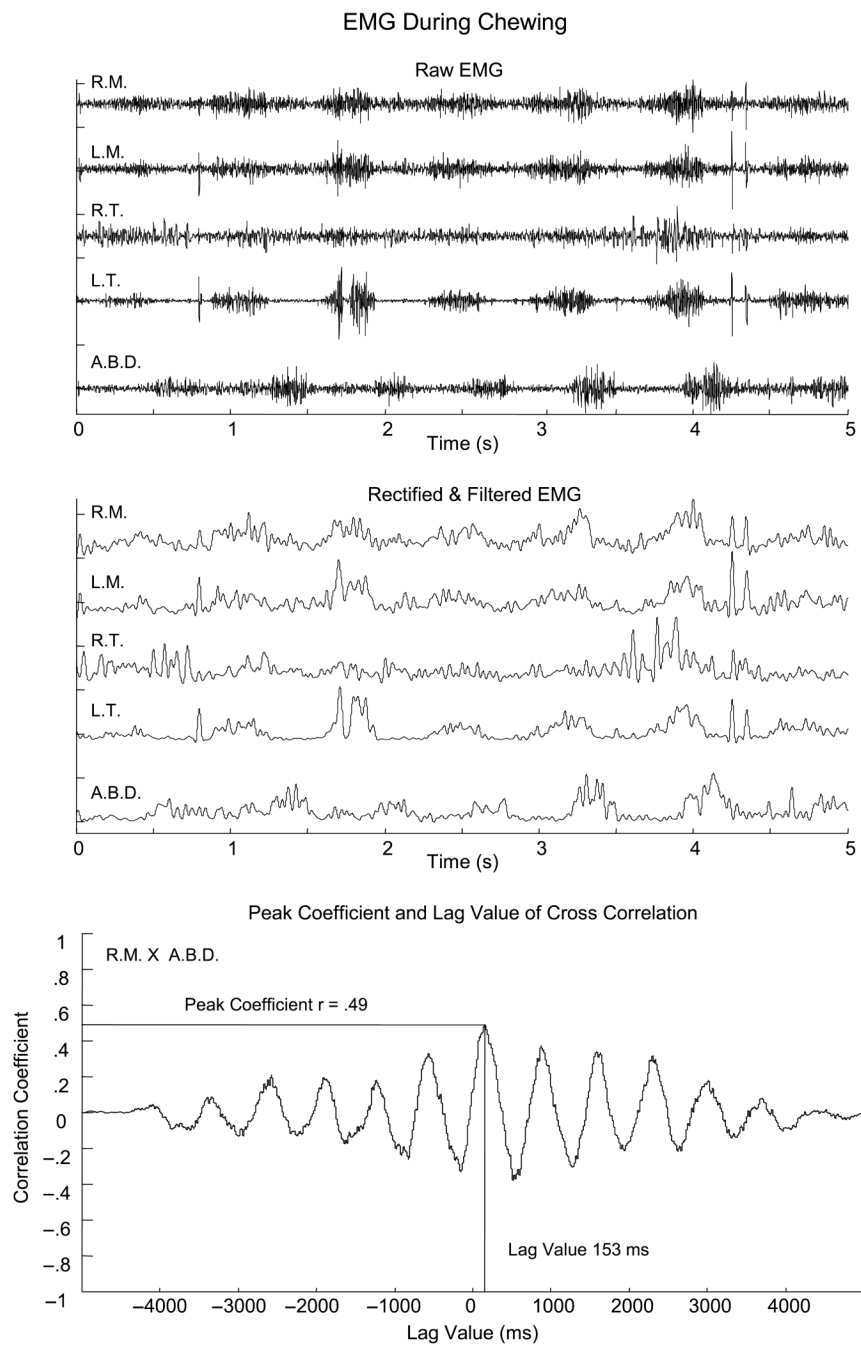


Figure 1. Illustrating the amplitude envelopes computed for each channel of electromyographic (EMG) and the cross-correlation function, which in this illustration was calculated between the right masseter (R.M.) and the anterior belly of the digastric (A.B.D). L.M. = left masseter; R.T. = right temporalis; L.T. = left temporalis.

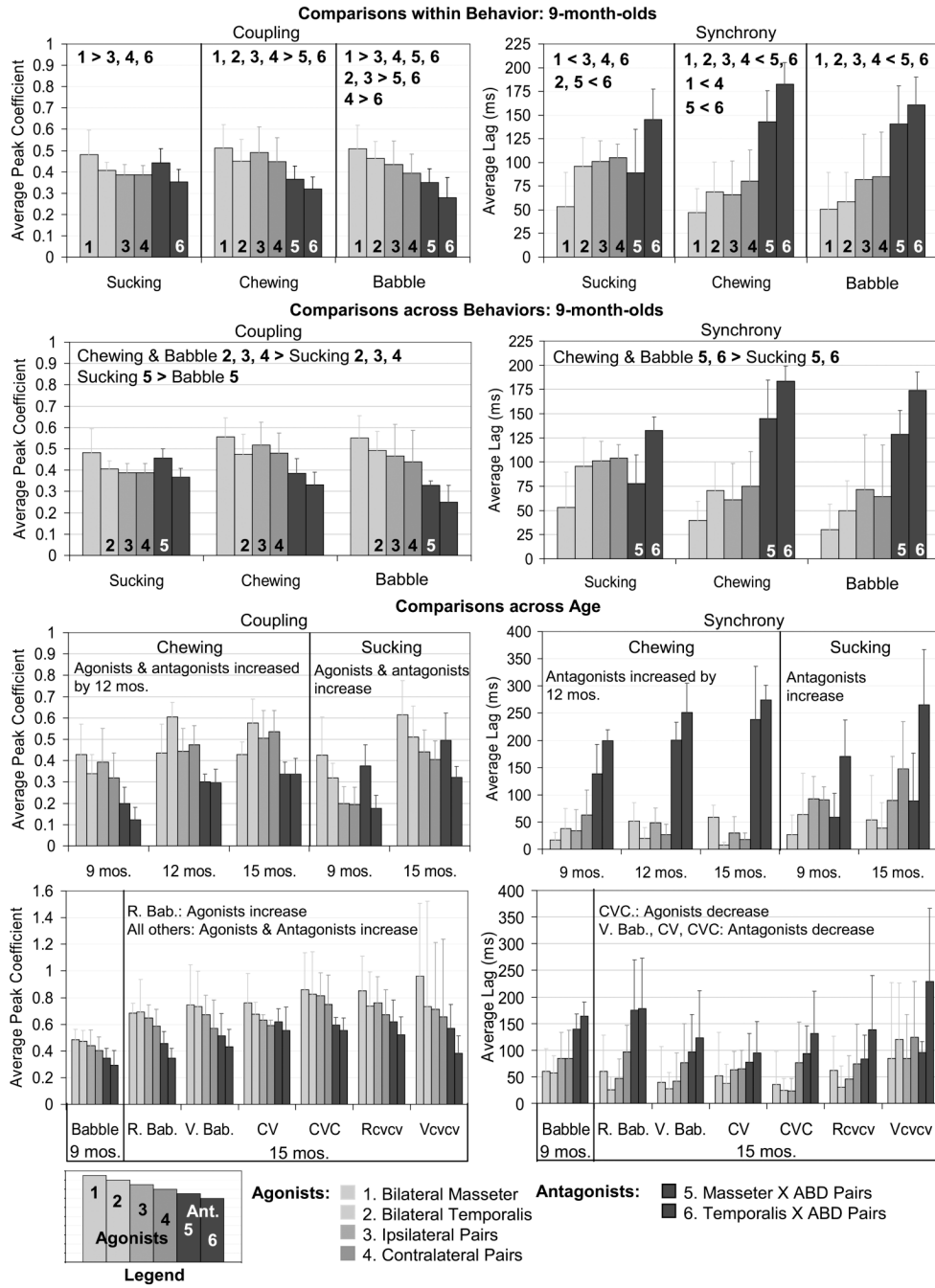


Figure 2. Vertical bars represent peak coefficients obtained from pairwise cross-correlations averaged across all repetitions and all subjects. Error bars are average within-subject standard deviations. From left to right, the first 4 vertical bars represent agonist (synergistic) muscle pairs, and the last two vertical bars represent antagonist pairs. R. Bab. = reduplicative babble; V. Bab. = variegated babble; ABD = anterior belly of the digastric; R = reduplicative; V = variegated.