Title: The dynamics of lingual-mandibular coordination during liquid swallowing.

Article Type: Original Article

Keywords: Deglutition; deglutition disorders; swallowing; tongue; jaw; coordination; electromagnetic articulography

Corresponding Author: Dr. Catriona M Steele, Ph.D.

Corresponding Author’s Institution: Toronto Rehabilitation Institute

First Author: Catriona M Steele, Ph.D.

Order of Authors: Catriona M Steele, Ph.D.; Pascal H Van Lieshout, Ph.D.
Running title: Lingual-mandibular coordination during liquid swallowing.

Title: The dynamics of lingual-mandibular coordination during liquid swallowing.

Authors: (1) Catriona M. Steele, Ph.D., SLP(C), CCC-SLP, Reg. CASLPO\textsuperscript{1,2}

(2) Pascal H.H.M. Van Lieshout, Ph.D. \textsuperscript{2,1}

Affiliations: (1) Toronto Rehabilitation Institute

(2) Oral Dynamics Laboratory, Graduate Dept. of Speech-Language Pathology, University of Toronto

Offprints: Catriona M. Steele,

Toronto Rehabilitation Institute,

550 University Avenue, #801,

Toronto, ON, Canada, M5G 2A2

Tel: (416) 597-3422 (X 3895)

Fax: (416) 597-3031

e-mail: steele.catriona@torontorehab.on.ca

Acknowledgements: Data collection for this manuscript was supported by a Natural Sciences and Engineering Research Council of Canada graduate student fellowship to the first author.

Manuscript preparation was supported by Toronto Rehabilitation Institute and a grant from the Ontario Ministry of Health and Long-Term Care. The views expressed do not necessarily reflect those of the ministry.
Abstract

Previous literature on tongue-jaw relationships during swallowing has focused on behaviors observed with chewable solid foods. The present investigation was undertaken to evaluate both the nature and stability of coordinative relationships between the jaw and three points located along the midsagittal groove of the tongue: anterior (blade), middle (body) and posterior (dorsum) during swallowing of thin and honey-thick liquids. A reiterative swallowing paradigm was used, with two task conditions (discrete and sequential), in order to explore the stability of tongue-jaw coordination across different frequencies of swallowing. Eight healthy participants in two age groups (young, older) performed sets of repeated swallows. Tongue and jaw movements were measured using electromagnetic midsagittal articulography. The data are analyzed in terms of variability in the spatio-temporal movement pattern for each fleshpoint of interest, and the temporal coupling (frequency entrainment) and relative phasing of movement for each tongue segment compared to the mandible. The results illustrate a stereotyped, but not invariant sequence of movement phasing in the tongue-jaw complex during liquid swallowing, and of task-related reductions in variability at higher frequencies of swallowing in tongue dorsum movements. This evidence supports the idea that different segments of the tongue couple with the jaw as a synergy for swallowing, but can modify their coupling relationship to accommodate task demands.

Key words:
Deglutition; Deglutition Disorders; Swallowing; Tongue; Jaw; Coordination; Electromagnetic Articulography
Introduction

Previous literature on tongue-jaw coordination in swallowing has focused primarily on relationships between these structures during the oral preparation, lingual propulsion and pharyngeal swallowing of chewable solid foods [1-4]. The current study was undertaken to explore the dynamics of coordination between the mandible and three different regions of the oral tongue (anterior, middle and posterior) during the swallowing of liquid stimuli. Our inquiry was motivated by two theoretical approaches, namely the motor control theory of Bernstein [5] and Coordination Dynamics theory (CD) [6]. These theories propose that motor behaviors involve the coupling (or linking) of different physiological structures (e.g. muscles) in task-specific control units known as synergies. A synergy is defined as a “highly evolved task-specific ensemble of neuromuscular and skeletal components constrained to act as a single unit” ([7], p.205) and provides a means of reducing mechanical degrees of freedom in a motor task [5, 8]. To provide an analogy, consider the design of an automobile with four wheels. In theory, each wheel could have a separate steering wheel to maximize flexibility. However, to ease the control of such a vehicle, engineers quickly decided to link the two wheels in the front, so they act as a single unit controlled by a single steering wheel and fix the two back wheels, so they are eliminated from the process of moving the vehicle in a specific direction. Hence the 4 possible degrees of freedom for vehicle control in the original design are reduced to one, which makes it safer and more efficient for human users. In short, coupling achieves solutions that balance the ease of control and required flexibility to keep a system efficient in achieving its task goal. The type of coupling mentioned in the automobile analogy is a structural one, and examples of structural synergies also exist in biological systems (e.g., combinations of bones, ligaments, muscles and joints). The majority of motor control synergies, however, are thought to be
temporary, flexible couplings, in which specific muscle systems are linked through a common neurological activation pattern related to specific task objective. For example, lip closure in speech production requires a functional coupling between the upper lip, lower lip and jaw. The task goal (i.e., a particular aperture of the space between the lips) can be achieved with varying contributions from the individual articulators depending on situational constraints [9, 10]. The selection and fine-tuning of preferred combinations for specific contexts is governed by principles of expediency, and influenced by circumstantial constraints [8]. Our hypothesis for this investigation was that different segments of the tongue (blade, body and dorsum) act cooperatively together and with the jaw during swallowing, and that coupling relationships evident between these structures would exhibit the hallmark characteristic of synergies, namely task-specific variation.

The tongue is a fluid-filled organ, attached to skeletal structures by three extrinsic muscles [11] and containing an intricate network of intrinsic muscles with vertical, longitudinal and transverse orientations [12, 13]. Perrier, Lœvenbruck and Payan [14] have described the shape of the tongue as dependent on the contributions of approximately 20 muscles; these include both the extrinsic and intrinsic muscles of the tongue, and all muscles connecting the tongue to the mandible, hyoid, pharyngeal walls and velopharynx. One MRI-based study of tongue contraction for swallowing [15] used internal strain-mapping and concluded that bolus accommodation involves the combination of intrinsic muscle contraction in the anterior tongue with extrinsic muscle contraction (genioglossus) in the posterior tongue. Bolus propulsion was associated with posterior passive stretch in the mid-sagittal plane suggesting contraction of the laterally inserted styloglossus muscle. Attempts to model tongue deformation during speech production tasks differ in the degree to which the complexity of the combined extrinsic and
intrinsic muscle contributions has been simplified [14, 16-22]. In the swallowing literature, most studies of tongue function have adopted a crude segmentation of the tongue into three or four regions, represented by discrete points along the midsagittal groove [3, 23-28]. Such simplification has been largely necessitated by the limitations of dynamic imaging techniques that have been used to study swallowing to date. While the videofluoroscopic studies of Hiiemae & Palmer [3] suggest that tongue rotation and lateral tongue movement are characteristic of tongue movements during the oral stage of solid food swallowing, previous ultrasound, MRI and biplanar videofluoroscopy studies suggest that events of interest during liquid swallowing occur largely along the midsagittal groove [15, 29-34]. In the current investigation, we adopted the same segmentation procedure as previous x-ray microbeam and videofluoroscopic studies [3, 23, 24, 26] and have measured movement of three points distributed in an anterior to posterior direction along the midsagittal groove of the tongue. Additionally, we have measured movement of the jaw, to permit exploration of relational characteristics between the behaviors of points on the anterior, middle and posterior tongue and the jaw in the hypothesized swallowing synergy. We will use terminology from the speech science literature [21, 35-38] to label the three selected tongue points respectively as the tongue blade (most anterior), tongue body (middle) and tongue dorsum (most posterior). It is acknowledged that this segmentation imposes artificial distinctions that do not reflect the complexity of the underlying musculature [12]. Furthermore, one cannot assume that the selected points necessarily represent distinct, homologus functional units in the tongue. Nonetheless, this approach does permit an understanding of the sequence of midsagittal tongue movement in a proximal (anterior/rostral) to distal (posterior/caudal) direction. Despite the hydrostatic ability of the tongue to deform, readers can be assured that the relative position of
the three selected markers (i.e., most anterior, middle and most posterior) remained constant throughout the reported experiments.

One experimental paradigm commonly used to expose the underlying parameters that govern the stability of synergies is to vary the rate with which a reiterated task is performed (e.g., [39-42]). By a reiterated task, we mean repeated performance of a motor act, such as finger tapping, or production of a particular phonetic string (e.g. “pa”). The expectation is that the task will be performed in a similar manner on each repetition (e.g. “pa pa pa pa pa pa”), but that rate manipulations might force the control system to change the nature of the coupling between the articulators in order to maintain stability in executing the task [6]. For example, in the task of closing the lips to produce the syllable “pa”, rate manipulations have been reported to affect the velocity profile of lip movements, such that slower productions involve more multipeaked profiles and faster productions involve more symmetrical, single peaked profiles [43]. In limb control studies it has been found that increasing the rate of movement can induce a transition from an anti-phase pattern of movement (such as the pattern of leg movement in a quadruped animal (e.g. a horse) while walking) to in-phase movement (as seen in quadruped running [44]). Similar findings have been reported for humans [6]. As these examples illustrate, task-specific variations in motor behaviors are reflected in transitions to new types of coupling behaviour that can be quantified in the phase relationship between cooperating structures.

An adaptation of the rate manipulation paradigm for studying motor control has previously been used to study tongue, floor-of-mouth muscle, and hyoid behaviors in swallowing; this adaptation involves the comparison of motor behaviors in discrete and sequential swallowing tasks [45-47]. Similar to the findings reported for other motor tasks, these studies have demonstrated reductions in the duration and amplitude of hyoid movement during
rapid sequential swallowing [47]. Sequential swallowing has also been reported to elicit shorter
tongue movement durations overall and greater temporal overlap between the activity of
functionally distinct segments of the tongue, seen in the onset of anterior tongue pre-propulsion
activities for subsequent boluses prior to the conclusion of posterior tongue movements for
previous boluses [46, 48]. These observations were interpreted to reflect simplification of the
swallowing motor sequence related to the performance of reiterated swallowing at higher
frequencies (swallows per second), suggesting plasticity in neuromotor control of the tongue and
related structures during swallowing [46-48]. We have adopted this same paradigm, to further
probe task-related differences in tongue and jaw behaviors in swallowing.

Research Questions

Three different aspects of tongue and jaw behavior were studied, as in previous studies of
oral movement in speech production [49]. First, knowing that a reiterative swallowing task
would elicit repetitive cyclic movement of each transducer of interest [27, 50], we were
interested in measuring variability (in both space and time) of the cyclic movement pattern
across task repetitions, and any fluctuations in this variability between discrete and sequential
swallowing. Consistent with previous observations of reduced variability in durational measures
of tongue-palate contact behaviors during sequential swallowing [47], we hypothesized that the
variability of segmental tongue and jaw movement would be reduced during reiterated sequential
swallows compared to reiterated discrete swallows.

Second, we were interested in determining whether the majority of participants would
display proximal-distal (or anterior to posterior) sequencing of movement across the three tongue
segments of interest (i.e. blade-body-dorsum) as reported by Gay and colleagues [26, 51]. We
were interested in documenting the extent to which movement sequencing remained stable, or
Coordinative Dynamics

varied, both across participants and as a function of swallowing task. We hypothesized that the
majority of participants would exhibit a blade-body-dorsum movement sequence within the
tongue and that this sequence preference would be unaffected by the swallowing task (discrete or
sequential swallowing).

Finally, we wanted to understand the coupling relationship between each of the three
tongue segments of interest and the jaw during liquid swallowing, and to explore whether this
coupling would become stronger [49, 52] or weaker [39, 53] at faster frequencies of reiterated
swallowing (i.e. sequential swallowing). Coupling strength is typically reflected in the motor
control literature using one of two characteristics: a) frequency entrainment, or b) the variability
of relative phase. Measures of frequency entrainment compare the degree to which specific
frequencies of oscillatory movement for two purportedly coordinated structures covary [54-58].
Correlations between the Fourier-transformed frequency spectra of two structures (in our case,
two transducer coil locations) are computed, and are considered to indicate the extent to which
the two structures are mutually driven by a common (set of) neural oscillator(s), by virtue of
their participation in a synergy [49]. Whereas measures of frequency entrainment reflect
consistencies in the temporal characteristics of movement for two cooperating structures, their
relative phase relationship reflects the nature and stability of coordination, or interdependency
between those two structures. In physics, *phase* is a term used to express the present position in a
cycle of something that changes cyclically. *Relative phase*, therefore, reflects the offset or
difference between the phases of two things that are changing cyclically. In the case of the
current investigation, relative phase represents the offset or difference between the positions of
two transducer coils that are moving in a cyclic fashion. High entrainment and a stable phase
relationship often co-occur, but more complex control systems may require flexibility in the
phasing between structures [59]. Previous research has suggested that oral articulatory structures become more tightly coupled and less variable in their phase relationships as the rate of task performance increases; evidence of this increased coupling strength is seen in tighter frequency entrainment while greater coordinative stability is seen in reduced relative phase variability [49]. For the present investigation, we expected this same pattern to be seen in tongue-jaw coupling during swallowing. We therefore hypothesized that the coupling relationships between each tongue segment and the jaw would display higher frequency entrainment and lower relative phase variability in sequential swallowing compared to discrete swallowing.

Methods

Participants

The current data are extracted from a larger dataset of oral movement data, collected from 8 adult volunteers (with no history or complaints of neurological impairment or swallowing difficulty) during the swallowing of 10 different liquid stimuli. The results of other analyses performed with this same dataset are reported elsewhere [27, 28, 60]. Based on previous literature describing increased variability in swallowing with normal aging [27, 61], two gender-balanced groups, each of 4 participants were recruited (young: mean age = 26.5; older: mean age = 59.25). All participants provided informed consent to participate, completed a brief medical history questionnaire, and passed a speech motor and swallowing screening performed by a registered speech-language pathologist (the first author).

Apparatus

Tongue and jaw movements during swallowing were transduced using an electromagnetic midsagittal articulograph (Carstens Medizin-Elektronik AG-100). Additional
details regarding this method of tracing oral movement in swallowing have been reported previously [27]. Movement data were acquired at 400 Hz for four transducer coils (each 2.4 mm in diameter), attached in midline to the mandibular incisors, and to midline points on the tongue blade, tongue body and tongue dorsum using a combination of surgical methacrylate resin (Cyanodent, Ellman International Mfg.) and zinc polycarboxylate dental cement (Durelon, Espe Dental AG). The targeted coil locations (see Figure 1) are comparable to those used in previous videofluorographic and x-ray microbeam studies of oral movement in swallowing [4, 23, 24] and were defined as 10 mm behind the anatomical tongue tip (blade), 40 mm behind the anatomical tongue tip (body) and 60 mm behind the anatomical tongue tip (dorsum). These positions were marked on the protruded tongue using a ruler and a dye stick prior to coil attachment. Coil position was subsequently measured during a resting posture, with the tongue held inside the mouth; as should be expected, some degree of contraction in the intercoil distance occurred upon retraction of the tongue into the mouth, with the final resting coil positions shown in Table 1. Reference coils were also attached to the nose, maxillary incisors, and upper and lower lips.

Following participant preparation, a helmet (62 cm in diameter) containing 3 electromagnetic transmitters was suspended from the ceiling above the participant and securely affixed to the participant’s head with a head-strap. These transmitters generate an alternating magnetic field within the helmet; an alternating voltage is induced in each transducer coil when it enters this magnetic field, allowing precise determination of the location of each coil [62]. The helmet is designed to follow any extraneous head movements closely; corrections for small deviations or rotations of the transducer coils away from midline are made using the signal of the third transmitter [63].
Experimental Procedure

Once ready, participants were handed a cup containing a liquid stimulus, and instructed to perform a series (henceforth termed trial-set) of 8 reiterated swallows of the liquid in either a discrete or sequential manner. Discrete trial-sets were performed by lowering the cup from the lips between each swallow; sequential trial-sets were performed in a continuous manner without lowering the cup from the lips between each swallow. The data reported in this manuscript comprise two discrete swallow trial-sets (i.e. 16 swallows) of thin apple-juice and two discrete swallow trial-sets of honey-thick apple juice for each of the 8 participants, and an equivalent number of sequential swallow trial-sets for each stimulus, yielding a total of 64 trial-sets (8 trial-sets X 8 participants) representing 512 individual swallows.

Data Processing

Data processing followed the same principles described for previous studies [27, 50, 57]. Movement data were first low pass filtered and then rotated so that the occlusal plane was aligned with the horizontal axis of the EMMA measurement field [64]. The position of each transducer coil (tongue blade, body, dorsum and mandible) was then calculated as the Euclidean distance from the nasal reference coil, as shown in Figure 1; this method for incorporating both X and Y displacement into measures of gestural position change has been previously used in the speech literature [59, 65, 66]. All movement data were then imported into MATLAB (Version 6.0.0.42a, Release 13, The Mathworks, Inc.) for further analysis.

All data were bandpass filtered between 0.1 and 6.0 Hz to remove drift and higher frequency noise from the movement trajectories. This setting preserves the relevant frequency information for the target behaviours in swallowing. Based on specific amplitude and window size criteria, the onsets and offsets of movement cycles for each transducer coil were indexed.
using an automated algorithm. These locations of peaks and valleys were verified visually and, if necessary, corrected by hand. This information was then used to derive the dependent variables for this study, as detailed below.

Variables

*Variability of the spatio-temporal movement pattern.*

Stability in the cyclic movement pattern for each individual transducer coil was quantified using a measure known as the cyclic spatio-temporal index, or cSTI [58]. The cSTI measure is based on a similar measure (the STI) [67], in which an index of spatiotemporal stability is derived by summing the standard deviations computed across amplitude- and time-normalized movement signals for a short speech utterance. The cSTI measure differs from the original measure by segmenting individual movement cycles as the unit of analysis (as opposed to linguistically defined data intervals), prior to amplitude- and time-normalization. Once normalized, the signals are aligned with each other and separate standard deviations for the overlapping segments are calculated at 2% intervals in relative time. The cSTI is defined as the sum of these standard deviations. Figure 2 illustrates the cSTI for tongue dorsum movement during sequential thin-liquid swallowing by a young female participant.

*Temporal coupling.*

Frequency entrainment between pairs of articulators was examined using a cross-spectral coherence analysis [54-56]. This technique measures the correlation between individual spectral bins of Fourier transformed position signals at a temporal resolution of 0.1 Hz [57]. Two signals are considered highly entrained if they consist of the same spectral components, and their spectral energy co-varies in time [49, 56]. Figure 3 illustrates two different examples of
frequency entrainment between the tongue dorsum and mandible from a young female participant. In the upper panel (A), data for a sequential swallowing trial-set are shown. Both coils share a dominant frequency peak at 1.2 Hz, and strong entrainment of the frequencies of their oscillations is seen (i.e., high cross-spectral coherence). The lower panel (B) illustrates a contrasting example from a series of discrete swallows. In this example, the dominant shared spectral peak lies at 0.5 Hz, but additional peaks at 0.8 and 1 Hz are shared between the signals. The strength of entrainment is weaker than in the first example, as shown in the lower cross-spectral coherence value.

<insert Figure 3 about here>

**Phase relationships.**

To explore the nature and stability of coordinative events in the swallowing sequence we calculated a continuous estimate of relative phase and its standard deviation for pairwise combinations of signals (each of the three tongue segments and jaw) [6, 58]. The movement signals were narrow band-pass filtered (+/- 0.25 Hz) around the shared dominant frequency for each pairwise signal combination (identified in the preceding cross-spectral coherence analysis). Phase-time functions were calculated on position- and velocity-normalized functions for each signal and used to calculate relative phase for the tongue blade, tongue body and tongue dorsum coils relative to the mandible. Figure 4 shows two contrasting examples of the relative phase relationship between tongue dorsum and mandible, taken from participant 4 (a young female) on two thin liquid trial-sets. The lower panel (B) represents discrete swallowing, and shows greater variation in the standard deviation of relative phase than the upper panel (A) representing sequential swallowing. In the present investigation, within-trial-set *standard deviation of relative phase* was used as an index of coupling stability.
Average relative phase was used to determine which of the two coils in each pairwise comparison (tongue, jaw) was leading. Relative phase values of 1° to 180° indicated that the tongue coil cycle preceded (or led) the jaw cycle, while values of 181-360° meant that tongue movement lagged behind the jaw. Relative phase values between the three tongue transducer coil positions and the common jaw referent were then compared to derive the order of each coil’s movement in the overall swallowing sequence. For example, relative phase values of 79°, 126° and 164° for the tongue blade, body and dorsum, respectively, represent a sequence of movement across the synergy commencing with the tongue blade, followed by the tongue body, then the tongue dorsum, and finally the mandible (see Figure 5 for an illustration of this sequence, including a relative phase diagram with a stylized version of the actual sequence).

Statistical Analyses

Statistical analyses were performed using SPSS 14.0 for Windows. The following variables were obtained for each trial-set of 8 repeated swallows: swallow frequency (swallows per second); the cyclic spatio-temporal index for each transducer coil (tongue blade, tongue body, tongue dorsum and mandible); mean cross-spectral coherence for pairwise combinations of each of the three tongue transducer coils with the mandible; mean relative phase for pairwise combinations of each of the three tongue transducer coils with the mandible; and within-trial-set standard deviation of relative phase for each tongue transducer coil paired with the mandible. Mixed design repeated measures analyses of variance (ANOVAs) were used to identify within-participant TASK (discrete vs. sequential) and STIMULUS (thin vs. honey-thick stimuli) differences, and between-participant COHORT (young vs. older) differences. The alpha level for statistical significance was set at \( \alpha = 0.05 \). When multiple comparisons were performed across
the different transducer coils and movement directions, a Bonferroni-corrected alpha of \( p < 0.03 \) was used [68]. Box’s M and Mauchly tests were conducted for all ANOVA results, to identify any violations of the assumptions of homogeneity of variance, covariance matrix circularity and compound symmetry; no such violations were found in the present data set. Effect sizes are reported for statistically significant findings using Cohen’s \( d \) standardized effect size, which is calculated as the difference in group means divided by the pooled standard deviation [69]. Effect size can be interpreted as strong for \( d \) values of 0.8 or higher, moderate for \( d = 0.5 \) to 0.79 and weak for \( d = 0.2 \) to 0.5 [70, 71]. The statistical inquiry into the predominance of patterns of entrainment and relative phase was conducted using Chi-Square analysis.

Results

Swallowing Frequency

Descriptive statistics for swallowing frequency (swallows per second) are shown in Figure 6. A repeated measures ANOVA with factors of COHORT under 30; over 50), STIMULUS (apple juice; honey-thick apple juice) and TASK (discrete; sequential swallowing) revealed significant main effects for all three factors: COHORT \( [F(1, 6) = 12.74, p = 0.012, d = 0.95] \); STIMULUS \( [F(1, 6) = 20.27, p = 0.004, d = 0.52] \); and TASK \( [F(1, 6) = 82.84, p = 0.000, d = 1.21] \). No statistically significant interactions were observed. Examination of these effects revealed lower frequencies of swallowing in the older participants compared to the younger, with the honey-thick stimuli compared to the thin apple juice, and during discrete swallowing compared to the sequential task. On average, participants swallowed almost twice as fast (ratio of 1.91:1) during sequential swallowing as during reiterated discrete swallows.
Cyclic Spatio-Temporal Index (cSTI)

Descriptive statistics for the cSTI are shown by coil position in Table 2. No statistically significant interactions and no main effects of COHORT were observed for any of the transducer coils. STIMULUS and TASK effects were not observed for cSTI of the mandible or the tongue blade. In the tongue body, significantly higher cSTI values (i.e. greater spatio-temporal variability) were observed with the honey-thick stimulus compared to the thin liquid \( F(1, 6) = 47.86, p = 0.001, d = 0.52 \). This STIMULUS effect was not observed in the tongue dorsum. A strong and statistically significant TASK effect was found, with greater spatio-temporal movement pattern variability seen in the discrete condition, both for the tongue body \( F(1, 6) = 9.95, p = 0.019, d = 0.77 \) and the tongue dorsum \( F(1, 6) = 16.07, p = 0.007, d = 0.87 \).

Frequency Entrainment (Cross-Spectral Coherence)

Means and standard deviations for cross-spectral coherence with the mandible are tabulated separately for the tongue blade, body and dorsum in Figure 7. Repeated measures ANOVAs were again performed for each tongue transducer coil with the same factors of COHORT, STIMULUS and TASK. No statistically significant differences were observed in the temporal coupling of the tongue blade to the mandible. For coupling of either the tongue body and tongue dorsum to the mandible, statistically significant effects were limited to the TASK factor. Higher mean cross-spectral coherence values (i.e. greater frequency entrainment) were observed in the sequential condition compared to the discrete task [tongue body: \( F(1, 6) = 29.52, p = 0.002, d = 0.84 \); \( F(1, 6) = 17.98, p = 0.005, d = 0.79 \)].
Phase Relationships

As shown in Table 3, a total of 9 different tongue segment movement sequences were derived from the mean relative phase values observed in the current data set. In the most prevalent sequence (observed 41% of the time), the tongue blade led the movement sequence, followed by the tongue body, then by the tongue dorsum and finally by the mandible. This pattern is illustrated in Figure 5, using data from a representative discrete honey-thick liquid trial-set. The second most common sequence (observed 38% of the time), was a simple variation on the most common sequence, in which tongue blade movement shifted from a leading position to one lagging the mandible by an average of 155°, thereby shifting the tongue body into leading position. Closer analysis of sequence frequencies for each individual participant in this study showed that the dominant sequence for each individual conformed to one of these two patterns. A further variation on this same movement order was observed 3% of the time, with the tongue dorsum leading the sequence and both the blade and body shifting to positions lagging movement of the mandible.

The third most commonly observed sequence differed in that mandibular movement advanced to a position leading (rather than lagging) movement of the tongue body and dorsum. This pattern was seen in 11% of the recorded trial-sets and interestingly occurred more than once in only 2 participants, both of whom were in the older cohort. The remaining 5 sequences were each only observed once in the entire data set, and their occurrence was isolated to discrete swallow tasks for participants in the older cohort. Chi-square analyses failed to identify any significant differences in the overall prevalence of the different phasing sequences as a function of TASK [$\chi^2 = 5.81, df = 8, p = 0.67$], STIMULUS [$\chi^2 = 9.19, df = 8, p = 0.33$], COHORT [$\chi^2 =$
14.89, \(df = 8, p = 0.06\), or across the eight individual participants \(\chi^2 = 66.789, df = 56, p = 0.15\).

Repeated measures ANOVAs (again with factors of \textit{COHORT}, \textit{STIMULUS} and \textit{TASK}) were performed separately for the three tongue transducer coils on the data for within-trial-set standard deviation of relative phase with the mandible. Figure 8 illustrates the mean values and 95% confidence intervals for standard deviation of relative phase with the jaw by cohort and task for each tongue coil. For the tongue blade, no significant effects were found. In the tongue body, significantly greater variation in relative phasing to the mandible was observed in older compared to younger participants \([F(1, 6) = 14.16, p = 0.009, d = 0.94]\), and in the discrete compared to the sequential condition \([F(1, 6) = 39.92, p = 0.001, d = 0.78]\). No significant interactions or \textit{STIMULUS} effects were seen. In the tongue dorsum, the only statistically significant effect was one of greater relative phase variation in the discrete condition \([F(1, 6) = 26.44, p = 0.002, d = 0.69]\).

<<insert Figure 8 about here>>

**Discussion**

To our knowledge, this is the first report in which the dynamics of coordination between the jaw and tongue have been explored during reiterated swallowing tasks with liquid stimuli. Our intent was to probe the stability of tongue and jaw movement patterns and their synergistic coupling using an experimental paradigm similar to the frequency-scaling experiments used commonly in the motor control literature (e.g., [39-42]). The data are taken from reiterated swallowing tasks, performed at varying participant-regulated rates, which clustered into two broadly defined categories of lower (discrete) and higher (sequential) swallowing frequencies. As predicted, increased frequencies of reiterated swallowing were associated with reduced
spatio-temporal variability in tongue and jaw movement (captured using the cSTI), increased
temporal coupling between the jaw and tongue (cross-spectral coherence), and decreased
variability in tongue-jaw coordination (relative phase). This study provides new evidence of
functional segregation within the tongue, with the predicted relationships holding true for
coupling of the mid and posterior portions of the oral tongue with the jaw, but not for the most
anterior (blade) portion. Furthermore, the observed reductions in movement variability and
relative phase variability at higher swallowing frequencies, coupled with increased posterior
tongue to jaw frequency entrainment, suggest a trend towards more global entrainment of the
different components of the tongue-jaw synergy at faster rates.

Within the literature, movement speed is considered to be one control variable that can
move a synergistic system from one stable coupling state to another [49]. As a system moves
between stable states, instability is commonly observed at bifurcation points, i.e. states of the
system where it is close to a transition [6, 53]. In the present analysis, we did not employ a
deliberate and continuous scaling of frequency; as such, it is not possible to speculate whether
the observed differences in the stability of relative phase and the degree of frequency
entrainment for the two swallowing tasks represent true dynamically induced fluctuations in
pattern stability. Nonetheless, the present results suggest that such fluctuations may be observed
in the swallowing motor sequence. The fact that single occurrences of atypical phasing
sequences were isolated to the older participants suggests the interesting possibility that motor
behaviors are more susceptible to exhibiting rate-related instabilities in older individuals. Future
studies in this regard will need to carefully consider effective means for controlling and scaling
swallowing frequency that remain safe for participants of all ages from the perspective of airway
protection.
On the basis of the predominance of certain patterns in the present data, we conclude that tongue movements in swallowing do, indeed, exhibit a strong trend towards following a stereotyped sequence, consistent with the predicted proximal-distal sequence of movement across the three lingual segments studied. This is consistent with the data reported by Gay, Rendell & Spiro [26]. Like Gay and colleagues [26], we did not observe pure adherence to a single serial sequence of tongue-jaw movement, but noted some variation with the mandible shifting its position relative to movement of the different tongue segments.

The data for this experiment were collected from participants in two age-cohorts using two stimulus consistencies (thin and honey-thick juice). Interestingly, while these factors significantly influenced the frequencies at which reiterative swallowing was performed, their influence was barely noticeable in the cSTI, frequency entrainment or phasing data. The only exceptions to this comment were seen in greater variability of tongue body phasing with the jaw in the older cohort, and in greater cSTI values in the tongue body with the honey-thick liquid compared to the thin liquid stimulus. One possible interpretation of this latter result is that the force demands inherent in propelling a denser and more viscous fluid into the pharynx involve a greater need for flexibility in spatio-temporal movement of the tongue body. The anatomical locus of these effects to the tongue body may also reflect greater importance of this region for bolus control in the presence of normal age-related changes in tongue muscle structure and function [72-74].

In summary, this coordinative dynamics analysis shows evidence of patterned behaviors in the tongue and jaw during swallowing with concurrent evidence of task-specific variations in these behaviors. Specifically, the task manipulation (i.e. discrete vs. sequential swallowing) yielded different patterns of effect in the tongue blade compared to the tongue body and dorsum.
Frequency entrainment and phasing between the tongue and jaw were susceptible to the influence of swallowing frequency. Consistent with the motor control literature, we observed greater frequency entrainment and a reduction in the variability of phase functions at higher swallowing frequencies. These data extend our understanding of normative function in swallowing motor control. This report is, to our knowledge, the first coordinative dynamics analysis of tongue and jaw coupling during liquid swallowing. The approach appears useful for the detection of patterned behaviors and their stability, and has potential to further inform our understanding of normal and pathological swallowing patterns in future studies comparing healthy and disordered individuals. In particular, the present results provide justification for future investigations of coupling stability across swallowing tasks of varying difficulty as a means of better understanding the nature of swallowing impairment and recovery.
References


Figure 1. EMMA transducer coil positions.

During electromagnetic midsagittal articulography studies of swallowing, transducer coils are attached in midline to the positions shown in the diagram on the left. Reference coils are denoted by the letter R. In the diagram on the right the method for calculating gestural position changes for EMMA transducer coils as a Euclidean distance relative to the nasal reference coil, as shown by the heavy XY line of the inset triangle for the tongue body. The same principle was applied to calculate Euclidean distance for the other transducer coil positions (mandible, tongue blade and tongue dorsum).
The cSTI is calculated as the sum of standard deviations taken at 2% intervals in relative time on the overlapped amplitude- and time-normalized segment waves. In this example, a highly stereotypical spatio-temporal movement pattern is seen for the tongue dorsum during sequential swallowing of a thin liquid stimulus; the associated (relatively low) cSTI value is 11.7.
Figure 3. Frequency Entrainment (Cross-Spectral Coherence).

Two examples of cross-spectral coherence between the tongue dorsum and mandible, taken from a young female participant. The upper panel (A) shows data for the tongue dorsum
(solid line) and mandible (dashed line) during a sequential swallow trial-set with thin apple-juice. Both transducer coils share a common dominant frequency peak at 1.2 Hz. The strong overall cross-spectral coherence relationship between these two coils (mean cross-spectral coherence = 95.8, SD = 1.91) is illustrated in the bottom bar of the panel; a value of 100 would represent pure entrainment across the entire spectrum. By contrast, the lower panel (B) illustrates data for a discrete trial-set, again with thin apple-juice, performed by the same participant. In this example, the tongue dorsum and mandible show a more complex spectral pattern with shared spectral peaks at 0.5, 0.8 Hz and 1 Hz. The overall cross-spectral coherence relationship is much weaker (39.3) and much more variable (SD = 33.4) than in the upper example.
Figure 4.

A. Amplitude Normalized Jaw Movement Signal

B. Amplitude Normalized Tongue Dorsum Movement Signal

Relative Phase Jaw (Degrees)

Relative Phase Tongue Dorsum (Degrees)

Relative Phase Jaw to Tongue Dorsum (Degrees)

Average Relative Phase = 222 degrees
SD Relative Phase = 9 degrees

Average Relative Phase = 226 degrees
SD Relative Phase = 8 degrees
Figure 4. Relative Phase Relationships.

Two examples of relative phase relationships between the tongue dorsum and mandible across a series of 6 completed movement cycles. The upper panel (A) shows data for the tongue dorsum (solid line) and mandible (dashed line) during a sequential swallow trial-set with thin liquid. The relative phase relationship is plotted in degrees in the lowermost bar of the panel, showing high stability with a mean value of 232° (SD = 9°). The lower panel (B) illustrates equivalent data from a discrete swallowing thin liquid trial-set from the same participant. In this example, the phase relationship between the tongue dorsum and mandible is very similar to that of sequential swallowing, but clearly more variable (mean = 235°, SD = 55°).
Figure 5.

See next page for figure caption.
Figure 5. Movement sequencing pattern.

The top bar of this figure illustrates the most commonly observed sequence order of tongue blade, body, dorsum and mandible movement derived from their relative phase relationships for a trial-set of discrete swallows with honey-thick juice. Below the phase diagram the corresponding movement traces are shown, clearly illustrating the pattern of movement across the four transducer coils, led by the tongue blade and followed by the tongue body, tongue dorsum and finally the mandible.
Figure 6. Means and 95% confidence intervals for swallowing frequency (swallows per second) during reiterated discrete and sequential swallowing of apple juice (open circles) and honey-thick apple juice (filled triangles) by healthy adults aged under 30 and over 50 years of age.
Figure 7. Means and 95% confidence intervals for cross-spectral coherence between three tongue segments (blade, body and dorsum) and the mandible during reiterated discrete (filled triangle) and sequential (open circle) swallowing.
Figure 8. Standard Deviation of Relative Phase (Jaw to Tongue)

Means and 95% confidence intervals for standard deviation of relative phase with the jaw are shown for each tongue segment (blade, body and dorsum) by age cohort (younger, older) and task (discrete vs. sequential swallowing). Statistically significant differences were seen between the younger and older participants for the tongue body, and between the discrete and sequential swallowing tasks for the tongue body and tongue dorsum.
Table 1. Coil positions (in distance from the anatomical tongue tip) at rest.

<table>
<thead>
<tr>
<th>Gender</th>
<th>Subject</th>
<th>Age</th>
<th>Tongue Blade (mm posterior to anatomical tongue tip)</th>
<th>Tongue Body (mm posterior to anatomical tongue tip)</th>
<th>Tongue Dorsum (mm posterior to anatomical tongue tip)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td>2</td>
<td>28</td>
<td>10.00</td>
<td>27.31</td>
<td>46.59</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>28</td>
<td>10.00</td>
<td>32.46</td>
<td>51.72</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>59</td>
<td>10.00</td>
<td>31.27</td>
<td>42.57</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>56</td>
<td>10.00</td>
<td>31.80</td>
<td>41.60</td>
</tr>
<tr>
<td>Males</td>
<td>1</td>
<td>27</td>
<td>10.00</td>
<td>38.95</td>
<td>44.78</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>23</td>
<td>10.00</td>
<td>31.87</td>
<td>46.02</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>66</td>
<td>10.00</td>
<td>36.11</td>
<td>45.65</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>56</td>
<td>10.00</td>
<td>33.63</td>
<td>57.04</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td>10.00</td>
<td>32.93</td>
<td>47.00</td>
</tr>
</tbody>
</table>
Table 2. Descriptive statistics for the Cyclic Spatio-Temporal Index shown by transducer coil.

<table>
<thead>
<tr>
<th>Task</th>
<th>Stimulus</th>
<th>Cohort</th>
<th>N*</th>
<th>Mandible</th>
<th></th>
<th>Tongue Blade</th>
<th></th>
<th>Tongue Body</th>
<th></th>
<th>Tongue Dorsum</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Discrete</td>
<td>Thin</td>
<td>Young</td>
<td>8</td>
<td>32.18</td>
<td>8.59</td>
<td>33.03</td>
<td>5.48</td>
<td>29.53</td>
<td>7.56</td>
<td>34.25</td>
<td>8.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Older</td>
<td>8</td>
<td>32.05</td>
<td>8.35</td>
<td>28.79</td>
<td>8.66</td>
<td>37.55</td>
<td>4.85</td>
<td>34.45</td>
<td>2.88</td>
</tr>
<tr>
<td>Honey-thick</td>
<td>Thin</td>
<td>Young</td>
<td>8</td>
<td>35.63</td>
<td>7.02</td>
<td>32.81</td>
<td>9.63</td>
<td>33.35</td>
<td>9.48</td>
<td>33.35</td>
<td>5.63</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Older</td>
<td>8</td>
<td>32.10</td>
<td>10.11</td>
<td>31.19</td>
<td>9.17</td>
<td>39.93</td>
<td>2.83</td>
<td>35.28</td>
<td>2.40</td>
</tr>
<tr>
<td>Sequential</td>
<td>Thin</td>
<td>Young</td>
<td>8</td>
<td>26.87</td>
<td>9.59</td>
<td>28.13</td>
<td>10.79</td>
<td>19.65</td>
<td>7.77</td>
<td>20.18</td>
<td>7.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Older</td>
<td>8</td>
<td>37.24</td>
<td>4.66</td>
<td>26.32</td>
<td>6.87</td>
<td>29.45</td>
<td>9.20</td>
<td>27.67</td>
<td>8.08</td>
</tr>
<tr>
<td>Honey-thick</td>
<td>Thin</td>
<td>Young</td>
<td>8</td>
<td>26.13</td>
<td>7.56</td>
<td>27.07</td>
<td>8.99</td>
<td>24.87</td>
<td>8.03</td>
<td>25.74</td>
<td>8.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Older</td>
<td>8</td>
<td>32.69</td>
<td>5.60</td>
<td>29.86</td>
<td>7.63</td>
<td>37.62</td>
<td>4.06</td>
<td>35.79</td>
<td>5.07</td>
</tr>
</tbody>
</table>

* N = the number of trial-sets. Each trial-set is a series of 8 reiterated swallows.
Table 3. Descriptive statistics for mean relative phase with the mandible for each of the tongue transducer coils, shown by observed movement sequence.

<table>
<thead>
<tr>
<th>Sequence</th>
<th>N</th>
<th>Tongue Blade</th>
<th></th>
<th>Tongue Body</th>
<th></th>
<th>Tongue Dorsum</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>Blade-Body-Dorsum-Mandible</td>
<td>26</td>
<td>24</td>
<td>19</td>
<td>94</td>
<td>34</td>
<td>125</td>
<td>34</td>
</tr>
<tr>
<td>Body-Dorsum-Mandible-Blade</td>
<td>24</td>
<td>335</td>
<td>20</td>
<td>62</td>
<td>33</td>
<td>117</td>
<td>37</td>
</tr>
<tr>
<td>Blade-Mandible-Body-Dorsum</td>
<td>7</td>
<td>35</td>
<td>41</td>
<td>204</td>
<td>32</td>
<td>237</td>
<td>37</td>
</tr>
<tr>
<td>Dorsum-Mandible-Blade-Body</td>
<td>2</td>
<td>290</td>
<td>24</td>
<td>337</td>
<td>31</td>
<td>13</td>
<td>17</td>
</tr>
<tr>
<td>Body-Blade-Dorsum-Mandible</td>
<td>1</td>
<td>32</td>
<td>N/A</td>
<td>25</td>
<td>N/A</td>
<td>82</td>
<td>N/A</td>
</tr>
<tr>
<td>Dorsum-Mandible-Body-Blade</td>
<td>1</td>
<td>334</td>
<td>N/A</td>
<td>270</td>
<td>N/A</td>
<td>16</td>
<td>N/A</td>
</tr>
<tr>
<td>Dorsum-Blade-Body-Mandible</td>
<td>1</td>
<td>29</td>
<td>N/A</td>
<td>151</td>
<td>N/A</td>
<td>2</td>
<td>N/A</td>
</tr>
<tr>
<td>Dorsum-Blade-Mandible-Body</td>
<td>1</td>
<td>48</td>
<td>N/A</td>
<td>340</td>
<td>N/A</td>
<td>21</td>
<td>N/A</td>
</tr>
<tr>
<td>Blade-Dorsum-Body-Mandible</td>
<td>1</td>
<td>12</td>
<td>N/A</td>
<td>24</td>
<td>N/A</td>
<td>16</td>
<td>N/A</td>
</tr>
</tbody>
</table>

N = the number of occurrences of each movement sequence in the data set.