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JAW ELEVATOR MUSCLE COORDINATION DURING RHYTHMIC MASTICATION IN PRIMATES: ARE TRIPLETS UNITS OF MOTOR CONTROL?

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Abstract

The activity of mammal jaw elevator muscles during chewing has often been described using the concept of the triplet motor pattern, in which triplet I (balancing side superficial masseter and medial pterygoid; working side posterior temporalis) is consistently activated before triplet II (working side superficial masseter and medial pterygoid; balancing side posterior temporalis) and each triplet of muscles is recruited and modulated as a unit. Here, new measures of unison, synchrony, and coordination are used to determine whether, in five species of primates (*Propithecus verreauxi*, *Eulemur fulvus*, *Papio anubis*, *Macaca fuscata*, and *Pan troglodytes*) muscles in the same triplet are active more in unison, are more synchronized, and are more highly coordinated than muscles in different triplets. Results show that triplet I muscle pairs are active more in unison than other muscle pairs in *Eulemur*, *Macaca*, and *Papio*, but triplet muscle pairs are mostly not more tightly synchronized than non-triplet pairs. Triplet muscles are more coordinated during triplet pattern cycles than non-triplet cycles, while non-triplet muscle pairs are more coordinated during non-triplet cycles than triplet cycles. These results suggest that the central nervous system alters patterns of coordination between cycles, recruiting triplet muscles as a coordinated unit during triplet cycles but employing a different pattern of muscle coordination during non-triplet cycles. The triplet motor pattern may simplify modulation of rhythmic mastication by being one possible unit of coordination that can be recruited on a cycle-to-cycle basis.

Keywords

chewing; unison; synchrony; coordination; relative phase

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6.5 AUTHOR CONTRIBUTIONS.

YR and CR designed the research; YR performed the research; YR and CR wrote and revised the paper.

6.2 STATEMENT OF ETHICS

All data were collected for prior studies, where relevant and appropriate Animal Welfare and IACUC information can be found.

6.3 DISCLOSURES

The authors have nothing to disclose. The authors certify that there is no actual or potential conflict of interest with this article. The objectivity of this research is not in any way compromised.

2. INTRODUCTION

Many species of animals chew, including some lizards [Ross et al. 2007], birds, and fish [Gidmark et al. 2014; Gintof et al. 2010], but most extant mammals chew in a fashion distinctive enough to warrant a special term, *mastication*. Primitively, mastication involved precise occlusion between the teeth with transverse tooth and jaw movements during food breakdown [Crompton 1971; Schultz and Martin 2014], and unilateral application of force to the food item on the working side (ws) of the tooththrow (the non-biting side is the balancing side (bs)) [Hiemäe 1976; Williams et al. 2011]. These features of mammalian mastication were present in stem Tribosphenida and are retained in many extant mammals, including the primates studied here. The transverse movements during jaw elevation are produced by asymmetric activation (amplitude and timing) of the jaw elevator muscles, including the superficial masseters (SM), posterior temporales (PT), and medial pterygoids (MP). Building on previous research [Gorniak 1977, 1985; Herring 1976; Herring et al. 1979; Herring and Scapino 1974; Weijs and Dantuma 1975], Weijs (1994) hypothesized that the bilateral activity of these three muscles during chewing is captured by the concept of a *triplet motor pattern* (Figure 1) in which the bSM (balancing SM), bMP (balancing MP), and wPT (working PT)—triplet I—are activated first, and the wSM (working SM), wMP (working MP), and bPT (balancing PT)—triplet II—are activated second [Weijs 1994]. He hypothesized that primitively mammalian mastication was characterized by activity of symmetrical vertical closers (SVCs) at the start of jaw elevation, followed by (and overlapping with) triplet I, which rotated the jaw towards the working side at the start of closing, followed by (and overlapping with) triplet II which rotated the jaw towards the balancing side at the end of closing, producing the transverse jaw movements characteristic of mammals. This motor pattern is seen in several groups of extant mammals, including primates, in which the triplet motor pattern has been identified in twelve out of sixteen species studied to date [Hylander and Johnson 1985; Hylander and Johnson 1994; Hylander et al. 1987; Hylander et al. 2004; Hylander et al. 2000; Hylander et al. 2011; Hylander et al. 2005; Langenbach and Hannam 1999; Ram and Ross 2018; Vinyard et al. 2006; Williams et al. 2011]. Across the mammals for which data are available, triplets I and II evolve together, suggesting that they perform an important functional role in mammal mastication [Williams et al. 2011].

The concept of the jaw elevator triplet motor pattern shares important similarities with the concepts of motor primitives [Giszter 2015] and muscle synergies [Tresch and Jarc 2009]. Like motor primitives, jaw elevator muscle triplets may function as “fundamental building blocks” for mastication, facilitating jaw muscle coordination and modulation, and like the muscle synergies of the locomotor cycle [Drew et al. 2008; Krouchev et al. 2006], jaw elevator muscle triplets are groups of muscles whose activity is coextensive during a particular phase of the gape cycle. Moreover, like the muscle synergies in the locomotor system [D’avella and Lacquaniti 2013; Drew et al. 2008; Krouchev et al. 2006; Overduin et al. 2014], there is reason to believe that species-specific jaw elevator motor programs “stored in the brainstem” [Weijs 1994] can be modulated—actively altered—by proprioceptive feedback and motor cortex [Dellow and Lund 1970; Lund et al. 1984; Lund and Kolta 2006; Westberg et al. 1998].

Modulation of jaw elevator muscle patterns by the CNS is essential for masticatory system function in the face of the changing properties of the food bolus during chewing sequences [Reed and Ross 2010; Vinyard et al. 2008]. Moreover, as mammals only possess one set of adult teeth, the ability to modulate muscle activity amplitude and relative timing is also important for minimizing tooth wear and the probability of tooth breakage. In fact, although triplets occur in the chewing cycles of many primates, analyses of variance show that there is more variation in muscle EMG activity patterns and jaw kinematics *within chewing sequences* on a single piece of food than *between chewing sequences* on different foods [Ross and Iriarte-Diaz 2014; Ross et al. 2012a; Vinyard et al. 2008]. There is also inter-specific variation in the proportion of cycles in which the triplet motor pattern is observed, as well as intra-cycle variation in the occurrence of the triplet motor pattern; e.g., the triplet motor pattern can characterize muscle activity onset, but not muscle activity offset [Ram and Ross 2018].

This raises important questions about the nature of the variability in jaw elevator motor patterns during mastication and its implications for motor control by the CNS. The goal of the present study is to ask: do jaw elevator muscle triplets function as units of motor control? Recent literature on muscle synergies addresses these questions, using a range of techniques designed to identify synergies (see [Tresch et al. 2006], for review), including associative clustering of muscle onset and offset phases followed by direct component analysis (DCA) [Drew et al. 2008; Krouchev and Drew 2013; Krouchev et al. 2006; Markin et al. 2012], and a range of linear decomposition methods, including nonnegative matrix factorization (NNMF) [Lee and Seung 1999; Overduin et al. 2014; Ting and Macpherson 2005; Tresch et al. 1999], and independent component analysis (ICA) [Hart and Giszter 2004].

In a previous paper, we documented in five species of primates the proportion of chewing cycles characterized by a triplet motor pattern, as well as the proportions of cycles in which the triplet pattern was evident at activity onset, peak, and offset [Ram and Ross 2018]. Our goal in the present study was not to identify muscle synergies in the feeding system, nor to determine whether jaw elevator triplets are muscle synergies in the sense used by previous workers. Rather, having identified cycles in which the triplet motor pattern occurs, we evaluated the degree to which, during natural feeding sequences, the CNS co-modulates the activity of jaw elevator muscle pairs in triplets more closely than it does non-triplet pairs. The animals' feeding systems were not experimentally perturbed in any way; rather, we leveraged natural variation in muscle activity associated with changing food bolus properties within feeding sequences to test three specific hypotheses:

1. Muscles in the same triplet are active more in unison than muscles in two different triplets;
2. Activity of muscles in the same triplet is more tightly synchronized than activity of muscles in two different triplets;
3. Muscles in the same triplet are more closely coordinated than muscles in two different triplets.

Definitions and mathematical tools

Testing hypotheses about cyclic phenomena benefits from use of mathematical tools used to study oscillations in dynamical systems: specifically, *continuous phase* (ϕ), a continuous and cumulative measure of an oscillator's progress through its cycle, and *relative phase* (ϕ_{1-2}), the relative timing of two oscillators. A $0^\circ \phi_{1-2}$ indicates that two signals are perfectly *in-phase synchronized* (or in *unison* with one another) while a $180^\circ \phi_{1-2}$ indicates that two signals are perfectly anti-phase synchronized.

Relative phase (ϕ_{1-2}) is used in both dynamical systems and neuroscience to quantify synchrony [Le Van Quyen et al. 2001; Pikovsky et al. 2001]. In the study of dynamical systems, synchronization is a *process*, the “adjustment of rhythms due to an interaction” (Pikovsky et al. 2001, xviii), characterized by frequency entrainment and phase locking. In the current study, two muscles are defined as being *synchronized* if specific events in their cycles (e.g., activity onset, peak, and offset) repeatedly occur with the same ϕ_{1-2} . Synchrony includes the case when two muscles reach specific events in their cycles—e.g., onset, peak, and offset—at the *same phase* in their cycles ($\phi_{1-2} = 0$). We refer to this subset of synchrony as *unison* and test for it by comparing the mean ϕ_{1-2} of two muscle pairs to the predicted ϕ_{1-2} of 0° . Synchrony also includes the more common cases when *different events* in the activity cycles of two muscles consistently occur at the *same phase*. For example, during human locomotion, maximum *flexion* of the left shoulder is synchronized with maximum *extension* of the right shoulder. It is important to note that synchrony is not all or nothing: statistical analyses can reveal relative degrees of synchrony. In the present case, activity in two muscles is perfectly synchronized if there is no variance in ϕ_{1-2} across all events (i.e., ϕ_{1-2} is constant but not necessarily equal to 0°), but of course, two muscles are never perfectly synchronized and the magnitude of variance in ϕ_{1-2} is a measure of the degree to which two oscillators are synchronized. Hence there are degrees or strengths of synchronization. This definition of a state of synchrony is compatible with the process of synchronization described by Pikovsky et al. (2001) because strong synchrony implies (a) mechanism(s) of synchronization. At present we are agnostic as to these mechanisms and only ask whether there is evidence of such synchronization in jaw elevator muscle triplets.

Coordination is a term often employed to describe interactions between multiple elements in a biological system, however strict definitions and standards for quantifying coordination are seldom applied. For example, Wainwright et al. [Wainwright et al. 2008] define coordination rather loosely as “association between movements of different body parts” (Wainwright 2008, 3524). Here we argue for a more precise and quantifiable definition of coordination that emphasizes the implication that coordination involves *active modulation of relative timing and amplitude*. We define muscle coordination as the *modulation (adjustment or maintenance)* of relative muscle activity (*amplitude and/or timing*) to achieve goal specific force production and kinematics [Konczak et al. 1997]. Even though one may not know what goals are actually being met, we argue that active modulation—coordination—is implied if the system co-modulates the activity of jaw elevator muscles in the context of variation in muscle firing patterns. In the present case, variation in muscle firing patterns within chewing sequences facilitates application of force and displacement to the food in such a way that it is broken down into a swallow-safe bolus while minimizing tooth wear and the risk of tooth

breakage. Hence, we propose that coordination between two muscles be quantified as the correlation coefficient (ϕ_1, ϕ_2) between the continuous phases (ϕ) of two muscles (1 and 2). Therefore, (ϕ_1, ϕ_2) measures two muscles' tendency toward co-modulation despite naturally occurring (unquantified) perturbations. Perfect unison and perfect synchrony can be subsets and manifestations of coordination, however, it is possible for two muscles to be coordinated without being synchronized or in unison if they both accumulate phase at different rates without modulating their activity with each other.

With these definitions in mind, this paper tests the following hypotheses regarding muscle activity patterns in jaw elevator muscle triplets.

Muscles in the same triplet are active more in unison than muscles in two different triplets.—This hypothesis predicts that muscles in the same triplet have a lower $\bar{\phi}_{1-2}$ than muscles in two different triplets; i.e., muscles in the same triplet are active with smaller differences in onset, peak, and offset times.

Activity of muscles in the same triplet is more tightly synchronized than activity of muscles in two different triplets.—This hypothesis predicts that muscles in the same triplet have a less variable ϕ_{1-2} than muscles in two different triplets, where variation in ϕ_{1-2} is measured as ϕ_{1-2} . This hypothesis addresses the possibility that although triplets may not reach onset, peak, and offset at the same time—in unison (see previous hypothesis)—they may be synchronized in maintaining constant *relative timing*.

Muscles in the same triplet are more closely coordinated than muscles in two different triplets: This hypothesis predicts that muscles in the same triplet will co-modulate their activity—have a higher (ϕ_1, ϕ_2)—than muscles in two different triplets. This hypothesis addresses the possibility that, although triplet muscles may not be active in unison, or be synchronized, their activity may still be co-modulated by the CNS.

Falsification of these hypotheses would argue against the idea that triplets I and II are units of control for the CNS.

GLOSSARY

	Metric	Abbreviation	Equation
	Continuous phase	ϕ_1	$H(t) = \frac{1}{\pi} \int_{-\infty}^{\infty} \frac{u(\tau)}{(t-\tau)} d\tau$ $\phi = \arctan\left(\frac{\text{real}(H(t))}{\text{imaginary}(h(t))}\right)$
	Relative phase (RP)	ϕ_{1-2}	$\phi_1 - \phi_2$
Unison	Mean RP (Single cycle)	$\bar{\phi}_{1-2}$	$\bar{\phi}_{1-2} = \frac{\sum_1^{100} \phi_{1-2}}{100}$
	Grand mean RP (All cycles)	$\bar{\bar{\phi}}_{1-2}$	$\bar{\bar{\phi}}_{1-2} = \frac{\sum_1^N \bar{\phi}_{1-2}}{N}$ N = number of cycles

	Metric	Abbreviation	Equation
	Standard deviation in grand mean RP	$\sigma_{\bar{\bar{\phi}}_1 - 2}$	$\sigma_{\bar{\bar{\phi}}_1 - 2} = \sqrt{\frac{\sum_1^N (\bar{\phi}_1 - 2 - \bar{\bar{\phi}}_1 - 2)^2}{N - 1}}$
Synchrony	Standard deviation in RP (Single cycle)	$\sigma_{\phi_1 - 2}$	$\sigma_{\bar{\phi}_1 - 2} = \sqrt{\frac{\sum_1^{100} (\phi_1 - 2 - \bar{\phi}_1 - 2)^2}{99}}$
	Mean standard deviation RP (All cycles)	$\bar{\sigma}_{\phi_1 - 2}$	$\bar{\sigma}_{\bar{\phi}_1 - 2} = \frac{\sum_1^N \sigma_{\bar{\phi}_1 - 2}}{N}$
	Standard deviation in standard deviation RP	$\sigma_{\bar{\sigma}_{\phi_1 - 2}}$	$\sigma_{\bar{\sigma}_{\bar{\phi}_1 - 2}} = \sqrt{\frac{\sum_1^N (\sigma_{\bar{\phi}_1 - 2} - \bar{\sigma}_{\bar{\phi}_1 - 2})^2}{N - 1}}$
Coordination	Correlation Coefficient	$\rho(\phi_1, \phi_2)$	$\rho(\phi_1, \phi_2) = \frac{1}{N - 1} \sum_1^N \left(\frac{\phi_1 - \phi_1}{\sigma_{\phi_1}} \right) \left(\frac{\phi_1 - \phi_1}{\sigma_{\phi_2}} \right)$

3. MATERIALS AND METHODS

Data selection

Data from three primate species—*Propithecus verreauxi*, *Papio anubis*, and *Macaca fuscata* — were downloaded from the FEED database [Wall et al. 2011]; data for *Eulemur fulvus* and *Pan troglodytes* were extracted from data files previously collected by one of us (CFR) in other studies. Sequences were selected for analysis if chewing side could be identified and the EMG data included the four triplet muscles analyzed and were of good quality (not clipped or too noisy). Sequences from the FEED database that had EMG data from bSM, wSM, bPT, and wPT were utilized in this study. MPt was excluded from this analysis because data for MPt were not available from many recording sessions, and cross-talk with the digastric was common in the MPt recordings that we did have (Figure 3 of a previous publication by the authors contains illustrations of the primary data utilized here [Ram and Ross 2018]). If chewing sequences in the FEED database included two channels of recordings from the same muscle, one of the two signals was arbitrarily chosen based on the following criteria: most constant baseline, least baseline noise, and largest unclipped amplitude during rhythmic mastication.

Chewing side was marked in the FEED database for chewing sequences from *Macaca*, *Papio*, and *Propithecus* (sequences were exclusively left or right chews). Chewing side for *Eulemur* was recorded on the voice track of the video or in experimental notes during data collection and corroborated using changes in principal strain orientation recorded from the mandible. In *Pan*, chew side was determined from the direction of jaw movement during the slow close phase of the gape cycle as seen on videos of the recording session: the mandible moving towards the left during slow close indicated a right chew and vice-versa. However, jaw movement was not visible for all chew cycles for *Pan*, so for the remaining cycles, a clustering algorithm that utilized EMG data for all jaw elevator muscles was used to determine ws. The clustering algorithm successfully classified all those cycles for which ws could be seen on video, so we proceeded under the assumption that all cycles in the two clusters were correctly assigned to ws.

Pre-processing

The data were full wave rectified and a 4th order low pass Butterworth filter with cutoff at 30 Hz was applied, followed by a root mean square (RMS) moving window integration with a 42 ms rectangular window moving one point at a time [Hylander and Johnson 1989]. Data were collected at 10 kHz except for *Eulemur* which was collected at 1 kHz. Cycle start and end were chosen manually such that all four channels had minimal EMG activity at the start of the cycle and each channel reached peak amplitude only once during each cycle. Every cycle was manually reviewed to ensure that no channels were clipped and all cycles represented only one complete cycle of jaw closing EMGs. FEED database characterization of left and right chews was used to change muscle names to include ws and bs. For Ross lab data, the experiment data sheet was used to identify the working and balancing sides and change the left and right superficial masseter and posterior temporalis to working and balancing side.

Calculation of continuous phase, ϕ

Channel amplitudes were normalized from -1 to 1 and all cycle lengths were normalized to 100 frames. The beginning and end of each sequence was padded with 1000 zeros then the Hilbert transform was used to calculate continuous phase. The Hilbert transform $H(t)$ of a signal is the convolution of the signal $u(t)$ with a filter $h(t) = 1/\pi t$ (equation 1).

The result of the Hilbert transform is an analytic signal with a real component that is equal to the original signal and an imaginary component equal to the convolution described above. For this study, the Matlab command “hilbert” was used to obtain this analytic signal. The continuous phase of the signal is equal to the arctangent of the real part of the analytic signal divided by the imaginary portion of the analytic signal (equation 2).

The resulting signal was then unwrapped using the unwrap function in Matlab and the extra 1000 zeros were removed from the beginning and end of the signal. The vector was then divided back into individual cycles with 100 frames each. The starting point of each cycle was set to zero by subtracting the original cycle phase at point 1 from all 100 points in the cycle. Only cycles with a final cycle continuous phase between 300 degrees and 420 degrees were used for all species except *Propithecus*. For *Propithecus*, the total number of degrees accumulated per cycle was consistently less than 260° and so this condition was omitted. All *Propithecus* cycles were used, regardless of final cycle continuous phase. For individual cycles, all 6 combinations of relative phase including the two SM and PT were calculated.

Unison

Only cycles that follow the triplet motor pattern were considered for this portion of the study. First, the mean relative phase ($\bar{\phi}_1 - 2$) for all muscle pairs was calculated within each cycle from the last onset time for any muscle to the first offset time for any muscle (defined as 25% of peak). The grand mean relative phase ($\bar{\bar{\phi}}_1 - 2$) for each pair was then calculated across all cycles. The p-values were calculated using a t-test to determine whether the mean RP of triplet pairs was significantly different ($p < 0.05$) from 0°. For each species, two criteria were used to determine whether muscles in the same triplet are more in unison than

muscles in two different triplets: (1) triplet I and triplet II muscle pairs must have a lower $\bar{\phi}_{1-2}$ than all other muscle pairs; and (2) the one-way t-test must show that muscles within the same triplet have a $|\bar{\phi}_{1-2}|$ distribution that is significantly different ($p = 0.008$) from that of all non-triplet muscle pairs. A Bonferroni correction was used to control against family-wise error rate. Additionally, a one-way t-test was used to test whether muscles within the same triplet have a $\bar{\phi}_{1-2}$ distribution that is not significantly different ($p = 0.05$) from 0° .

Synchrony

Only cycles that follow the triplet motor pattern were considered for this portion of the study. First, the standard deviation in relative phase ($\sigma\bar{\phi}_{1-2}$) for all muscle pairs was calculated within each cycle from the onset of the last muscle (25% of peak amplitude) to offset of the first muscle (25% of peak amplitude). Then, the mean standard deviation in relative phase ($\bar{\sigma}\bar{\phi}_{1-2}$) was calculated across all cycles. A one-way t-test was used to make pairwise comparisons between the $\sigma\bar{\phi}_{1-2}$ of muscles in the same triplet versus the muscles in two different triplets. For each species, two criteria were used to determine whether muscles with the same triplet are more synchronized than muscles in two different triplets: (1) triplet I and triplet II muscle pairs must have lower $\bar{\sigma}\bar{\phi}_{1-2}$ than all other muscle pairs; and (2) the t-test must show that muscles within the same triplet have a $\sigma\bar{\phi}_{1-2}$ distribution that is significantly different ($p = 0.008$) from all non-triplet muscle pairs. Once again, a Bonferroni correction was used to control family-wise error rate.

Coordination

The degree of coordination between two muscle pairs was measured by the correlation between ϕ of two muscles across all triplet cycles and a one-sample Kolmogorov-Smirnov test was used to ensure that the distribution of $\rho(\phi_1, \phi_2)$ was normal. Triplet muscles were more coordinated than non-triplet muscles if the $\rho(\phi_1, \phi_2)$ of triplet muscles was higher than that of non-triplet muscles. The $\rho(\phi_1, \phi_2)$ for each muscle pair was also calculated for each cycle. A one-way t-test was used to determine if the triplet muscles had a significantly higher ($p = 0.008$) distribution of (ϕ_1, ϕ_2) during triplet and non-triplet cycles compared to non-triplet muscle pairs. A Bonferroni correction was used to control family-wise error rate.

4. RESULTS

A cycle follows the triplet motor pattern if all the muscles in triplet I reach peak activity before all the muscles in triplet II. Table 1 shows the number of cycles considered per individual and the number of cycles that followed the triplet motor pattern.

Unison

Figure 3 and Table 2 show the $\bar{\phi}_{1-2}$ (in degrees) for all muscle pairs in all five species. Triplet muscles are more in unison if they have a lower $\bar{\phi}_{1-2}$ than non-triplet muscles and a $|\bar{\phi}_{1-2}|$ distribution that is significantly different ($p = 0.008$) from all other muscle pairs. Triplet muscles are in unison if the $\bar{\phi}_{1-2}$ is not significantly different from zero ($p = 0.05$).

In *Eulemur*, triplet muscle pairs had the lowest $\bar{\phi}_1 - 2$. However, the $|\bar{\phi}_1 - 2|$ distribution of neither triplet I nor triplet II was significantly different from all other muscle pairs ($p = 0.0476$ for triplet I and $p = 0.0705$ for triplet II). Both triplet pairs have a $\bar{\phi}_1 - 2$ that is not significantly different from 0° ($p = 0.1934$ and $p = 0.5135$ for triplet I and II respectively based on a t-test). These results suggest that both triplet pairs are active in unison in *Eulemur*, but neither triplet is more in unison than non-triplet pairs.

In *Propithecus*, triplet pairs are not more in unison than non-triplet pairs. A non-triplet muscle pair (wPT-wSM) has the lowest $\bar{\phi}_1 - 2$ (14.70°), however, this muscle pair also has the largest standard deviation in $\bar{\phi}_1 - 2$ (70.13°). Triplet II but not triplet I has a $|\bar{\phi}_1 - 2|$ that is significantly lower than all non-triplet muscle pairs ($p = 0.1248$ for triplet I and $p = 0.0062$ for triplet II). However, the $\bar{\phi}_1 - 2$ for both muscle pairs is significantly different from 0° ($p = 0.0055$ for triplet I and $p = 0.0168$ for triplet II). Thus, for *Propithecus*, triplet muscles are not more in unison than non-triplet muscles.

In *Papio*, triplet I has the lowest $\bar{\phi}_1 - 2$ ($6.93 \pm 15.30^\circ$) and a significantly lower $|\bar{\phi}_1 - 2|$ than all non-triplet muscle pairs (triplet I $p < 0.0001$). Both triplet I and triplet II have $\bar{\phi}_1 - 2$ distributions that are significantly different from 0° ($p = 0.0407$ for triplet I and $p < 0.0001$ for triplet II). Thus in *Papio*, triplet I but not triplet II is significantly more in unison than non-triplet muscles.

In *Macaca*, triplet I but not triplet II has a lower $\bar{\phi}_1 - 2$ than all other muscle pairs ($\bar{\phi}_1 - 2 = 5.78 \pm 20.70^\circ$ for triplet I, $\bar{\phi}_1 - 2 = 30.96 \pm 19.00^\circ$ for triplet II). Triplet I also has a lower $|\bar{\phi}_1 - 2|$ distribution than non-triplet muscle pairs ($p < 0.0001$ for triplet I). Neither triplet I nor triplet II were in perfect unison ($p < 0.0001$ for triplet I and $p < 0.0001$ for triplet II). In *Macaca*, only triplet I is more in unison than non-triplet pairs.

In *Pan*, both triplet I and triplet II has the lowest $\bar{\phi}_1 - 2$ ($\bar{\phi}_1 - 2 = -7.36 \pm 31.49^\circ$ for triplet I, $\bar{\phi}_1 - 2 = -13.22 \pm 28.65^\circ$ for triplet II). But neither triplet I nor triplet II has a $|\bar{\phi}_1 - 2|$ distribution that was significantly lower than that of non-triplet muscles ($p = 0.3829$ in triplet I and $p = 0.4357$ for triplet II). Triplet I but not triplet II has a $\bar{\phi}_1 - 2$ that was not significantly different from 0° ($p = 0.1824$ for triplet I and $p = 0.0111$ for triplet II). Thus, while triplet I may be active in unison in *Pan*, neither triplet I nor triplet II is more in unison than non-triplet muscles.

Synchrony

Figure 4 and Table 3 show the $\bar{\sigma}_{\phi_1 - 2}$ (in degrees) for all muscle pairs in all five species. In *Macaca*, triplet I but not triplet II has a lower $\bar{\sigma}_{\phi_1 - 2}$ than non-triplet muscle pairs ($p < 0.0001$). Thus in *Macaca*, triplet I but not triplet II is more synchronized than non-triplet muscles. In the other four species studied, both triplet I and triplet II did not have a $\bar{\sigma}_{\phi_1 - 2}$ that is lower than the $\bar{\sigma}_{\phi_1 - 2}$ of non-triplet muscles.

Coordination

One-sample Kolmogorov-Smirnov tests showed that the distribution of $\rho(\phi_1, \phi_2)$ for all muscle pairs in all species was normal. Figure 5 and Table 4 show the $\rho(\phi_1, \phi_2)$ for the six jaw elevator muscle pairs across all triplet cycles. In *Eulemur*, *Papio*, *Macaca*, and *Pan*, the six jaw elevator muscle pairs have $\rho(\phi_1, \phi_2)$ ranging from 0.97270 to 0.9962. In *Pan* Triplet II is more coordinated than all other muscle pairs; (ϕ_{WSM} , ϕ_{bPT}) is higher than all other $\rho(\phi_1, \phi_2)$ by 0.0013 to 0.0075 but triplet I is less coordinated than all other triplet pairs ($\rho(\phi_{bSM}$, $\phi_{wPT}) = 0.9757$). In *Macaca* triplet I is more coordinated than all other muscle pairs; (ϕ_{bSM} , ϕ_{wPT}) = 0.9947 is higher than all other $\rho(\phi_1, \phi_2)$ by 0.0004 to 0.0181. In all other species, the $\rho(\phi_1, \phi_2)$ of triplet muscle pairs is neither the highest nor the lowest (ϕ_1, ϕ_2). *Propithecus* has the most variability in jaw muscle coordination across the six jaw elevators; *Propithecus* $\rho(\phi_1, \phi_2)$ range from 0.8303 to 0.9786. Triplet I muscle pairs are more coordinated than triplet II muscle pairs in all species except *Pan*.

To get a more thorough understanding of the degree to which triplet muscles are coordinated compared to non-triplet muscle pairs, Tables 5–9 show the distribution of $\rho(\phi_1, \phi_2)$ for triplet and non-triplet pairs in triplet and non-triplet cycles. Two-way t-tests are used to identify significant differences ($p = 0.008$).

In *Eulemur*, triplet muscle pairs have a lower mean $\rho(\phi_1, \phi_2)$ and standard deviation in $\rho(\phi_1, \phi_2)$ during triplet cycles compared to non-triplet cycles ($p = 0.004$): triplet muscles are more coordinated during triplet cycles than during non-triplet cycles. However for non-triplet muscle pairs neither the mean $\rho(\phi_1, \phi_2)$ nor the standard deviation in $\rho(\phi_1, \phi_2)$ differs significantly between triplet and non-triplet cycles.

In *Papio*, there are no significant differences in the coordination of triplet and non-triplet muscles between triplet and non-triplet cycles. However, during triplet cycles, the mean $\rho(\phi_1, \phi_2)$ of triplet muscles is significantly higher than non-triplet muscles ($p = 0.007$) and the standard deviation in $\rho(\phi_1, \phi_2)$ for non-triplet muscles is double that of triplet muscles. During non-triplet cycles there are no significant differences between triplet and non-triplet muscles in $\rho(\phi_1, \phi_2)$ ($p = 0.976$). Thus, in *Papio* triplet muscles are more coordinated than non-triplet muscles during triplet cycles.

In *Macaca*, triplet muscles are more coordinated during triplet cycles than in non-triplet cycles ($p < 0.001$), and they have both a lower mean $\rho(\phi_1, \phi_2)$ and higher standard deviation in $\rho(\phi_1, \phi_2)$ during non-triplet cycles. Non-triplet muscles are more coordinated during non-triplet cycles than triplet cycles ($p < 0.001$), and they have both a lower mean $\rho(\phi_1, \phi_2)$ and a higher standard deviation $\rho(\phi_1, \phi_2)$ during triplet cycles.

Unlike the three species listed above, in both *Propithecus* and *Pan*, there are no significant differences in the coordination of triplet muscles during triplet and non-triplet cycles.

5. DISCUSSION

In this study, succinct, quantifiable definitions of unison, synchrony, and coordination are proposed and used to test hypotheses regarding the role the CNS plays in modulating the

relative timing and amplitude of jaw muscle activity. We hope that these definitions and the variables used to quantify them will, by formalizing future discussions, help to advance studies of coordination and synchronization in musculoskeletal biomechanics and motor control. By employing measures of continuous relative phase, our quantification of degrees of unison, synchrony and coordination applies across the entire cycle [Kelso 1995], not to discrete measures of relative phase, such as those embedded in some analyses of muscle synergies [Krouchev and Drew 2013; Krouchev et al. 2006]. Relative phase has been used in multiple fields of study to quantify the interaction between two cyclic signals. Here, this measure was used to quantify the degree of co-modulation between muscle pairs. We proposed succinct and quantifiable definitions of unison, synchrony, and coordination that can be widely used to describe the interaction or degree of co-modulation between any two entities that repeatedly move in a stereotyped manner. This includes muscle pairs, joints (e.g., the shoulder and the wrist during reach and grasp), kinematic markers, and even neural populations. Relative phase assumes that the signal is sinusoidal or unimodal. For example, if a muscle bursts twice within a single cycle, it will accumulate 720° of continuous phase as oppose to 360° . In the present study, we eliminated all muscle activity prior to onset and after offset to make the signal more sinusoidal and ensure that each muscle accumulates approximately 360° per cycle.

Implicit in our use of continuous RP to address our hypotheses is the assumption that the CNS uses the gape cycle as a unit of control, so that synchronization and coordination might be controlled at the level of the entire cycle. Indirect support for this assumption comes from the fact that mammals chew and locomote with low variance in cycle duration compared to lepidosaurs, crocodilians and amphibians, suggesting that cycle duration is actively modulated in the interests of sensorimotor predictability [Ross et al. 2010; Ross et al. 2012b]. That said, our use of continuous RP did require that the muscle activity profiles be constrained to a sinusoidal form, necessitating exclusion of cycles that violated this assumption—e.g., multiple peaks of activity within a gape cycle.

Despite the limitations of continuous relative phase, application of these definitions and techniques does suggest new insight into jaw elevator muscle triplets in the feeding systems of primates, namely, the degrees to which these triplets are in unison, synchronized and coordinated vary between species. Previous research demonstrated that the triplet motor pattern occurs more frequently than expected by random probability in *Eulemur*, *Propithecus*, *Papio*, *Macaca* and *Pan* [Ram and Ross 2018]. However there is variation in the timing of muscle activation within a single cycle. The present study utilized succinct quantifiable definitions of unison, synchrony, and coordination to falsify the hypothesis that the triplet motor pattern forms a unit of control for the CNS in *Eulemur*, *Propithecus*, *Papio*, and *Pan*. Incidentally, in the previous study, only *Macaca* exhibited the triplet motor pattern at onset of muscle activity, peak muscle activation, and offset of muscle activity [Ram and Ross 2018]. The current study suggests that only in *Macaca* are triplet muscles more highly coordinated during triplet cycles and non-triplet muscles are more tightly coordinated during non-triplet cycles..

Implications for jaw elevator motor control in primates

The fact that triplets are not characterized by stereotyped patterns of activation means that triplet motor patterns are not *invariant* units of control for the CNS [Overduin et al. 2008]. Different patterns of coordination predominate in different cycles for different species. In *Propithecus*, *Papio*, *Macaca*, and *Pan*, even when the triplet motor pattern is observed, the triplet muscles are not consistently in unison, synchrony, or coordinated. These findings suggest that triplets do not form a unit of control for *Propithecus*, *Papio*, *Macaca*, or *Pan*.

However, in *Macaca*, triplets do appear to function as facultative units of control, their activity being coordinated during some chewing cycles and not others. Even in *Macaca*, they appear to be flexibly recruited, appearing in some cycles and not others. The fact that triplet muscles are more coordinated during triplet cycles compared to non-triplet cycles but they are not more tightly synchronized suggests that active modulation (presumably based on sensory feedback) may be functionally important during some *times* in the cycle but not others. A different pattern of coordination that does not require a triplet motor pattern appears to be utilized during non-triplet cycles, leading to increased coordination between non-triplet muscle pairs in *Macaca*.

These findings suggest that the system recruits a range of motor patterns, but the intrinsic criteria used by the system to assess which motor pattern to recruit are unknown. Future EMG studies should be aimed at defining the full range of jaw elevator motor patterns and their relationship to jaw kinematics throughout chewing sequences with the hope of uncovering the extent to which various optimality criteria affect the system and the neural factors that may influence specific muscle activation patterns [Mussa-Ivaldi et al. 1990]. Inclusion of data from medialpterygoid would be an important test of the results presented here.

Triplets as a Movement Primitive in *Macaca*

The fact that triplet I muscles are active in unison and coordinated suggests that they may form a *movement primitive* or module in *Macaca*. Movement primitives have been proposed as a solution to the “ill posed” problem [Mussa-Ivaldi et al. 1990]; i.e., for any given movement there is an infinite combination of muscle activation strategies that would produce the observed or desired kinematics [Mussa-Ivaldi et al. 1990; Vinyard et al. 2008]. It is hypothesized that movement primitives provide a mechanism for the CNS to bootstrap complex problems to identify optimal patterns of muscle activation. However, unlike triplet I, triplet II is neither synchronized nor coordinated in any of the species studied, suggesting that the CNS regulates triplet I more tightly than it does triplet II.

From the neural and motor control perspectives, motor primitives can serve one of two functions: They may be a constraint on movement control, or they may be an optimization strategy [Nazarpour et al. 2012]. The first implies that motor patterns are conserved due to hard-wired neural circuitry. The second implies that because any movement of a body part is influenced by similar biomechanical principles, the optimal muscle synergies and/or motor primitives will be broadly conserved [Nazarpour et al. 2012]. If conservation in motor patterns is a result of optimization, then any repertoire of muscle synergies and/or motor

primitives stored in the CNS would serve as a reserve of optimal shortcuts as opposed to neural constraints on behavior.

Computational neuroscientists have proposed that motor primitives called muscle synergies may be used by the CNS to simplify motor control, where muscle synergies are defined as “coordinated recruitment of groups of muscles with specific activation profiles” [D’Avella and Lacquaniti 2013]. While the concept of muscle synergies is closely related to the motor primitives suggested here, there are some key differences in the methods used to identify and test for them. Muscle synergies are identified by decomposing muscle activations into temporal sequences of vectors using factorization techniques, including non-negative matrix factorization (NNMF) and independent components analysis (ICA) [d’Avella and Bizzi 2005; Tresch and Jarc 2009]. However, as has been pointed out, the muscle synergies identified using these techniques may more closely reflect task constraints and parameters rather than neural control strategy [Tresch and Jarc 2009].

Rather than utilizing statistical techniques to identify recurring patterns of muscle activation (within the limited task of jaw closing), the current paper tests the degree of interaction between muscles in a very specific pattern of muscle activation. The benefit of the relative phase method is that it quantifies both the interaction between muscles and the relative degrees of variation in the interaction between muscles. We do not assume that the triplet motor pattern is a unit of motor control: indeed, the results of the current study suggest that jaw elevators are flexibly recruited and that triplet motor patterns are not invariant units of control for the CNS.

An alternative to the muscle synergy hypothesis is the controlled manifold or minimum intervention hypothesis. This hypothesis suggests that variability in muscle activation patterns does not reflect errors but represents efficient control by allowing variability in dimensions that are not task related [Tresch and Jarc 2009]. In the present case, the controlled manifold hypothesis would corroborate the observation that even when the triplet motor pattern is observed in *Eulemur*, *Propithecus*, *Papio*, and *Pan*, the triplet muscles are not in unison, synchronized, or coordinated. The present findings suggest that in these four species, the CNS does not actively control for the presence of the triplet motor pattern. Studies also suggest that variability observed during specific tasks is best explained by modifying the activity of individual muscles as opposed to muscle synergies [Kutch et al. 2008]. While the controlled manifold and muscle synergy hypotheses are not mutually exclusive, the controlled manifold hypothesis more closely aligns with the results observed in the current study. Moreover, unlike the muscle synergy hypothesis, the controlled manifold hypothesis allows for the activity of specific muscles to be modified independently based on sensory feedback. Further investigations of muscle activity patterns in the jaw and hyolingual muscles of mammals promise new perspectives and insight into the control of movement by the central nervous system.

EQUATIONS

$$H(t) = \frac{1}{\pi} \int_{-\infty}^{\infty} \frac{u(\tau)}{(t - \tau)} d\tau \quad \text{Equation 1}$$

$$\phi = \arctan\left(\frac{\text{real}(H(t))}{\text{imaginary}(h(t))}\right) \quad \text{Equation 2}$$

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Fig. 1.

Weijs (1994) hypothesized that jaw elevation in primates is produced by a combination of movement modules known as triplet I and triplet II. He predicted that the primitive mammalian motor pattern (A) is observable in extant strepsirrhines while extant anthropoids display the transverse motor pattern (B).

Unison, Synchrony, and Coordination Between Muscle Pairs

Fig. 2. Continuous phase of two muscles that are in unison, synchrony, and coordinated plotted. The dotted line shows the relative phase of two muscles that are perfectly in unison with each other. The dashed line shows the relative phase of two muscles that are perfectly synchronized with each other but not in unison. Finally, the solid line shows the relationship between two muscles that are coordinated but not in unison or synchrony. Perfect unison and synchrony can be subsets of coordination.

Are muscles in the same triplet more in unison than muscles in two different triplets?

Fig. 3. The $\bar{\phi}_{1-2}$ for all cycles that follow the triplet motor pattern.

To determine whether muscles within the same triplet are more in unison than muscles in two different triplets, we calculated the $\bar{\phi}_{1-2}$ between muscle pairs for individual cycles, then took the $\bar{\phi}_{1-2}$ across all cycles. A positive $\bar{\phi}_{1-2}$ means that the muscle listed first fired before the second muscle. A negative $\bar{\phi}_{1-2}$ means that the muscle listed second became active first.

Are muscles in the same triplet more in synchrony than muscles in two different triplets?

Fig. 4. The $\bar{\sigma}_{\phi_{1-2}}$ for all triplet cycles.

To determine whether muscles within the same triplet are more synchronized than muscles in two different triplets, we calculated $\sigma_{\phi_{1-2}}$ for all muscle pairs in a cycle. We then calculated $\bar{\sigma}_{\phi_{1-2}}$ for all triplet cycles.

Are muscles in the same triplet more coordinated than muscles in two different triplets?

Fig. 5. The $\rho(\phi_1, \phi_2)$ for all triplet cycles.

To determine whether muscles within the same triplet are more coordinated than muscles in two different triplets, we calculated $\rho(\phi_1, \phi_2)$ for all muscle pairs across all triplet cycles.

Table 1.

Number of Cycles per Individual

Species	Individual	N cycles with triplets	N cycles total
<i>Eulemur fulvus</i>	B	17	60
	H	10	71
<i>Propithecus verreauxi</i>	C	46	57
<i>Papio anubis</i>	M	10	14
	G	5	6
	C	8	15
<i>Macaca fuscata</i>	B	76	172
	S	35	119
	T	101	183
<i>Pan troglodytes</i>	O	13	43
	A	21	84

Table 2.Unison: Mean RP $\bar{\phi}_{1-2}(\circ)$

	Triplet I	Triplet II	Non Triplet Pairs			
	bSM - wPT	wSM - bPT	bSM - wSM	wPT - bPT	bSM - bPT	wPT - wSM
<i>Eulemur</i>	$5.68 \pm 22.10^\circ \vee$	$2.73 \pm 21.43^\circ \vee$	$20.38 \pm 22.46^\circ$	$17.43 \pm 21.98^\circ$	$23.11 \pm 30.79^\circ$	$14.70 \pm 9.34^\circ$
<i>Propithecus</i>	$23.28 \pm 54.10^\circ$	$14.56 \pm 39.76^\circ \wedge$	$29.58 \pm 38.41^\circ$	$20.87 \pm 52.56^\circ$	$44.14 \pm 19.82^\circ$	$6.30 \pm 70.13^\circ$
<i>Papio</i>	$6.93 \pm 15.30^\circ \wedge$	$40.84 \pm 29.65^\circ$	$24.01 \pm 12.46^\circ$	$57.92 \pm 33.08^\circ$	$64.85 \pm 35.52^\circ$	$17.07 \pm 13.38^\circ$
<i>Macaca</i>	$5.78 \pm 20.70^\circ \wedge$	$30.96 \pm 19.00^\circ$	$23.46 \pm 19.26^\circ$	$48.63 \pm 24.98^\circ$	$54.42 \pm 28.50^\circ$	$17.67 \pm 16.63^\circ$
<i>Pan</i>	$-7.36 \pm 31.49^\circ$	$-13.22 \pm 28.65^\circ \vee$	$16.15 \pm 24.76^\circ$	$10.28 \pm 30.02^{**}$	$2.93 \pm 26.66^{**}$	$23.50 \pm 32.09^\circ$

$\wedge$ the distribution of $|\bar{\phi}_1 - 2|$ for the triplet muscle pair is significantly lower than that of non-triplet pairs ($p < 0.008$) (based on a one-way t-test).

$\vee$ the $\bar{\phi}_1 - 2$ of the triplet pair is not significantly different from 0° ($p > 0.05$) (based on a one-way t-test)

Table 3.Synchrony: Standard Deviation in RP $\bar{\sigma}_{\phi_{1-2}}$ (°)

	Triplet I	Triplet II	Non Triplet Pairs			
	bSM - wPT	wSM - bPT	bSM - wSM	wPT - bPT	bSM - bPT	wPT - wSM
<i>Eulemur</i>	8.15 ± 5.38°	7.26 ± 6.88°	8.90 ± 6.65°	8.13 ± 6.22°	9.60 ± 8.52°	6.92 ± 5.00°
<i>Propithecus</i>	22.21 ± 26.52°	13.57 ± 20.30°	10.55 ± 18.34°	25.27 ± 28.74°	11.33 ± 7.34°	28.23 ± 30.17°
<i>Papio</i>	8.20 ± 8.02°	9.09 ± 7.61°	6.74 ± 6.50°	11.97 ± 11.23°	13.51 ± 10.21°	7.06 ± 5.62°
<i>Macaca</i>	5.73 ± 4.58°*	9.36 ± 5.33°	7.83 ± 6.37°	12.70 ± 8.38°	14.25 ± 9.87°	6.81 ± 4.99°
<i>Pan</i>	13.40 ± 11.34°	9.53 ± 5.43°	12.74 ± 7.52°	11.63 ± 10.16°	12.89 ± 8.25°	12.31 ± 9.77°

* distribution of $\sigma_{\phi_{1-2}}$ of triplet muscles is significantly less than that of non-triplet muscles (p 0.008) (based on a one-way t-test)

Table 4.Coordination: Correlation Coefficient $\rho(\phi_1, \phi_2)$

	Triplet I	Triplet II	Non Triplet Pairs			
	bSM - wPT	wSM - bPT	bSM - wSM	wPT - bPT	bSM - bPT	wPT - wSM
<i>Eulemur</i>	0.9880	0.9874	0.9896	0.9957	0.9856	0.9973
<i>Propithecus</i>	0.8888	0.8766	0.9446	0.8303	0.9469	0.9786
<i>Papio</i>	0.9950	0.9776	0.9871	0.9962	0.9945	0.9720
<i>Macaca</i>	0.9947	0.9817	0.9918	0.9943	0.9921	0.9766
<i>Pan</i>	0.9757	0.9803	0.9832	0.9770	0.9815	0.9819

Table 5.Eulemur $\rho(\phi_1, \phi_2)$

	Triplet Cycle	Non Triplet Cycle	
Triplet Pairs	0.996 ± 0.005	0.993 ± 0.008	$p = 0.004^*$
Non Triplet Pairs	0.994 ± 0.009	0.994 ± 0.009	$p = 0.828$
	$p = 0.056$	$p = 0.2909$	

Table 6.Propithecus $\rho(\phi_1, \phi_2)$

	Triplet Cycle	Non Triplet Cycle	
Triplet Pairs	0.964 ± 0.70	0.979 ± 0.027	$p = 0.332$
Non Triplet Pairs	0.958 ± 0.073	0.979 ± 0.032	$p = 0.062$
	$p = 0.532$	$p = 0.957$	

Table 7.Papio $\rho(\phi_1, \phi_2)$

	Triplet Cycle	Non Triplet Cycle	
Triplet Pairs	0.992 ± 0.007	0.991 ± 0.008	$p = 0.423$
Non Triplet Pairs	0.986 ± 0.014	0.991 ± 0.010	$p = 0.043^*$
	$p = 0.007^*$	$p = 0.976$	

Table 8.Macaca $\rho(\phi_1, \phi_2)$

	Triplet Cycle	Non Triplet Cycle	
Triplet Pairs	0.995 ± 0.005	0.992 ± 0.008	$p < 0.001^*$
Non Triplet Pairs	0.988 ± 0.012	0.993 ± 0.008	$p < 0.001^*$
	$p < 0.001^*$	$p < 0.001^*$	

Table 9.Pan $\rho (\phi_1, \phi_2)$

	Triplet Cycle	Non Triplet Cycle	
Triplet Pairs	0.990 ± 0.014	0.988 ± 0.013	$p = 0.312$
Non Triplet Pairs	0.989 ± 0.014	0.991 ± 0.010	$p = 0.139$
	$p = 0.582$	$p = 0.015^*$	