Preference and consequences: A preliminary look at whether preference impacts oral processing in non-human primates

Christopher J. Vinyard^a, Cynthia L. Thompson^b, Alison Doherty^c, Nicholas Robl^d

^a Department of Anatomy and Neurobiology, NEOMED.

^b Department of Biomedical Sciences, Grand Valley State University.

^c WWAMI Medical Education Program, University of Wyoming.

^d Southwest Wildlife Conservation Center.

Corresponding Author:

Email address: cvinyard@neomed.edu

Key words: Food preference, Electromyography, Food mechanical properties, Muscle, Feeding

Pages: 26 Tables: 3 Figures: 5

Abstract

Non-human primates demonstrate food preferences much like humans. We have little insight, however, into how those preferences impact oral processing in primates. To begin describing this relationship, we conducted a preliminary analysis measuring food preference in two tufted capuchins (*Cebus apella*) and comparing ranked preference to physiological variables during chewing of these foods. Food preference was assessed for each monkey across 12 foods, including monkey biscuits and 11 foods consumed by humans (e.g., various fruits and nuts). Animals chose from randomized pairs of foods to generate a ranked scale across the 12 foods. Contemporaneous with preference testing, electromyographic (EMG) activity was measured for the jaw-closing muscles to assess oral physiology during chewing of these foods. As expected, these capuchins exhibited clear preferences among these 12 foods. Based on their preferences, we identified sets of preferred and non-preferred brittle (i.e., almond versus monkey chow) and ductile (i.e., dates and prunes versus apricots) foods for physiological comparisons that broadly control variation in food mechanical properties (FMPs). As expected, oral physiology varied with FMPs in each animal. Within brittle and ductile groupings, we observed several significant differences in chewing cycle length and relative muscle activation levels that are likely related to food preference. These differences tended to be complex and individual specific. The two capuchins chewed non-preferred apricots significantly faster than preferred dates and prunes. Effect sizes for preference were smaller than those for FMPs supporting the previous focus on FMPs in primate dietary research. Although preliminary, these results suggest that food preference may influence oral physiology in non-human primates. The prospect that this relationship exists in monkeys raises the possibility that a link between food preference and oral processing in humans may be based on shared tendencies with non-human primates, such as aversion to bitter items or preference for sweet foods.

Introduction

The pioneering work on food mechanics by Lucas and colleagues (Darvell, 1996; Lucas et al., 2000; Lucas, 2004) has provided primatologists with a number of tools and approaches for empirically documenting variation in primate food mechanical properties (FMPs). These studies have markedly shifted how we think about both primate diets and the ways that primates reduce foods (Kinzey & Norconk, 1990; Lucas, 2004; Berthaume, 2016). In fact, many researchers hypothesize that FMPs have played a role in driving the interspecific variation in masticatory apparatus form across primates (e.g., Hylander 1979; Ravosa, 1991; Taylor, 2002; Lambert et al., 2004; Wright, 2005; Constantino and Wright, 2009; but see Ross et al., 2012).

We know that variation in FMPs impacts oral processing within individuals and species based on physiological studies of feeding mechanics (e.g., Horio and Kawamura, 1989; Hylander et al., 1987, 2000; Agrawal et al., 1998; Foster et al., 2006; Vinyard et al., 2006; Reed and Ross, 2010). This influence of mechanical properties demonstrates that food texture, which combines mechanical, structural and surface properties of foods (Szczesniak, 2002; Lawless and Heyman, 2010), has a significant influence on feeding behaviors. Texture is perceived by animals and can include auditory cues (e.g., the crispness of chips), visual textures (e.g., fruit color denoting ripeness) as well as oral sensations perceived during chewing (e.g., hardness of foods).

Following the ground-breaking work of Lucas and colleagues, we explore how food preference potentially impacts oral processing. Non-human primates certainly exhibit food preferences much like humans (Hladik and Simmen, 1996; Simmen and Hladik, 1998; Visalberghi et al., 2003; Remis, 2002; Hladik et al., 2003). We know very little, however, about

how preference influences oral processing in any primate species. Recent work in humans has identified four groups of consumers that differ in mouth behaviors: 1) crunchers, 2) chewers, 3) smooshers and 4) suckers (Jeltema et al., 2014, 2015)¹. Non-human primates also exhibit variation in food preference within species (e.g., Simmen and Hladik, 1998; Remis, 2002). These different feeding styles likely have consequences for oral processing in terms of chewing speed and jaw-muscle recruitment patterns. Although not linked to these mouth behavior groups, previous electromyographic (EMG) research on the jaw adductors from a large sample of humans identified four major groupings of oral processors based on variation in chewing speed and muscle recruitment (Brown et al., 1994). Taken together, the Jeltema et al. (2014, 2015) and Brown et al. (1994) studies promote an intriguing possibility for links between behavioral preferences and oral processing in humans. In this study, we examine whether food preference has a significant impact on oral processing in two tufted capuchins (*Cebus apella*) as a preliminary examination of this potential relationship in primates.

Materials and Methods

Subjects

We assessed preference and oral processing in two capuchins (*Cebus apella*). Both were adult males born in captivity that exhibited no obvious dental trauma. Capuchin C was a young adult male exhibiting significant postcanine crown relief, while capuchin M was older with worn postcanine teeth. Each participated readily in preference testing and fed readily during oral physiology studies.

¹ These categories describe how different consumers prefer to interact with foods during feeding. This paradigm was developed to describe preferred mouth behaviors of consumers for product development and marketing (Jeltema et al 2015).

88

89 *Preference*

90 We measured preference among 12 foods following Visalberghi (2003) (see also Silberge
91 et al., 1998) (Table 1). The two capuchins were familiar with all foods prior to preference
92 testing. Animals were housed in separate cages in the same room eliminating the impact of
93 dominance on food choice. Foods were shaped to approximately the same size and kept out of
94 view prior to testing. Fruits were dried, with the exception of apples, which were fresh.
95 Randomized pairs of foods were placed one in each hand and shown to an animal from about a
96 meter's distance for approximately 5 seconds to allow the animal to visualize the two foods.
97 We then moved the foods within reaching distance and allowed the animal to choose one food
98 item in this two-alternative choice test. The unselected item was removed. After 3 minutes, if
99 no food was selected then a new combination was presented. We then recorded whether the
100 monkey consumed the foods, partially consumed it, or discarded it. If discarded, we waited
101 approximately one minute and began another trial. We performed 5-7 trials per day and
102 presented each combination of foods 5 times for each monkey (66 possible pairs x 5 = 330 total
103 trials). Testing typically occurred prior to daily feeding helping to standardize any impact of
104 hunger across days. Randomizing pairs of food presented likely reduced the impact of satiation
105 on preference across the experiment.

106

107 *Jaw-muscle electromyography*

108 Procedures for constructing and implanting electrodes, as well as collecting
109 electromyographic (EMG) data, follow Hylander et al. (2000). Prior to inserting electrodes, we
110 sedated each animal with a combination of medetomidine (0.06 mg/kg) and ketamine (7.0
111 mg/kg) and seated it in a restraint chair that allowed free head and neck movement. Animals
112 were habituated to restraints before collecting jaw-muscle EMG data. We used fine-wire,

bipolar indwelling electrodes (nickel-chromium alloy, 0.05 mm diameter; California Fine Wire) to record jaw-muscle activation.

We inserted electrodes in the superficial masseter and temporalis muscles on both sides. Following electrode implantation, we allowed the animal to recover from anesthesia. Once the animal was alert, we fed it the various foods described in Table 1 until sufficient data were collected or the animal was satiated. EMG potentials were amplified, band pass filtered (100 – 3,000 Hz) and recorded to a computer at 10 kHz. Following data collection, we reanesthetized the animal, removed the electrodes and returned the animal to its cage. We completed five successful experiments for each animal (n=3,274 chewing cycles). EMG experiments were conducted separately from preference testing.

We calculated the root-mean-square (rms) of the raw EMG signal using a 42 millisecond (ms) time constant at 2ms intervals (see Fig.2 in Hylander et al., 2000) to produce a single EMG waveform for analysis. We then identified the largest peak rms value per electrode across all chewing cycles in an experiment and assigned it a value of 1.0. The remaining smaller peaks were linearly re-scaled to this value for each electrode. Thus, for each cycle we generated a relative estimate of peak EMG activity that can be compared across electrodes and experiments (Hylander et al., 2000). We used synchronized video to determine the chewing side and separately considered scaled peak EMG activity for the working-side, or chewing-side, and balancing-side, or non-chewing side, muscles. Finally, we estimated chewing cycle length as the time between consecutive peaks of the chewing-side superficial masseter (WSM) during rhythmic mastication.

Analyses

We determined food preference in the two capuchins by ranking the number of times a food was chosen across all comparisons (of 55 total per food) followed by pairwise comparison to break ties. We compared preferences between monkeys using a Spearman's rank order

correlation ($\alpha=0.05$). Based on these rankings, we chose preferred/non-preferred brittle and ductile foods for considering how preference may impact oral processing. By considering pairs of brittle and ductile foods separately, we attempted to control significant aspects of food mechanical properties to focus on how preference impacts oral processing.

Prior to considering how preference impacts oral processing, we examined whether oral processing parameters changed during an experiment. Following Woda et al., (2006) and Thompson et al. (2011), we considered chewing cycle length as a summary measure of oral processing. To facilitate comparison across multiple experiments, we mean-centered cycle lengths for each capuchin prior to analysis of cycle length changes within an experiment. Additionally, we examined scaled peak EMGs for each jaw muscle. We performed an ANCOVA ($\alpha=0.05$) for food mechanical property groupings (i.e., ductile or brittle foods) with trial number throughout an experiment as the covariate to control for oral processing parameters that changed consistently during an experimental session.

To examine how preference impacts oral processing, we compared preferred to non-preferred ductile and brittle foods, respectively, for each capuchin. We compared cycle length and scaled peak EMG parameters using an ANOVA ($\alpha=0.05$) or ANCOVA ($\alpha=0.05$) with trial number as a covariate when oral processing variable changed consistently throughout an experiment. Statistical analyses were conducted using Systat 13.0.

Results

Do capuchins exhibit food preferences?

The two capuchins demonstrated clear food preferences (Table 1). Capuchin M preferred raisins, dates and prunes while capuchin C exhibited preference for almonds, dates and peanuts. Both animals disliked monkey chow and apricots (Table 1). Capuchin M demonstrated greater selectivity as he did not choose a food in 55 (of 330) trials. Alternatively, capuchin C chose a food in all trials. Preference rankings between the two capuchins were

significantly correlated (Spearman's $\rho = 0.77$, $P=0.003$). Based on preference rankings, we chose a brittle food comparison of almonds versus monkey chow as almonds were always chosen over monkey chow by both animals. Similarly, dates (and prunes for capuchin M) were always chosen over apricots providing the ductile food comparison. While brittle foods had similar elastic moduli (E) (almonds: $E=19.4$ MPa; monkey chow: $E=50.4$ MPa) and ductile foods had similar toughness (R) values (prune: $R=345.7$ J m⁻²; apricot: $R=506.3$ J m⁻²) (Williams et al., 2005), other aspects of food material properties likely vary between these pairwise comparisons.

Does oral processing change throughout a feeding experiment?

Chewing cycle length varied with animal, ductile versus brittle food mechanical properties (FMP) groupings and trial number (Fig. 1). For capuchin M, FMP grouping ($t=5.27$, $P<0.001$) was significant while trial was not ($t=-0.44$, $P=0.66$) ($n=44$). ANCOVA for capuchin C considering chewing cycle length showed significant effects of FMP groupings (i.e., ductile versus brittle) ($t=3.93$, $P<0.001$) and trial ($t=-2.90$, $P=0.006$) ($n=40$). Capuchin C chewed a given food item more quickly as an experiment progressed (Fig. 1). Interactions were not significant for either animal ($P>0.05$). ANCOVAs for scaled peak EMGs for the masseter and temporalis did not show a consistent relationship with trial number during an experiment. Only a single instance, the working-side temporalis in capuchin M, showed a relationship with trial number ($t=-2.33$, $P=0.025$). This association did not persist after an adjusted-Bonferroni correction for multiple comparisons. Peak muscle activities consistently differed with FMP groupings in these two animals (results not shown).

Does preference impact oral processing?

We assessed preference and oral physiology parameters for brittle (i.e., almond versus monkey chow) and ductile (i.e., date and prune versus apricot) foods separately as foods within

these categories have broadly similar FMPs (Table 2, Figs 2, 3). ANOVA of mean-centered cycle lengths shows that capuchin M chewed preferred almonds significantly slower than monkey chow ($F=59.75$, $P<0.001$, $n=830$) (Fig. 2). Alternatively, capuchin C chewed preferred almonds significantly faster than non-preferred monkey chow (ANOVA: $F=9.76$, $P=0.002$; Covariate = trial, $n=640$) (Fig. 2). Capuchin M chewed preferred, ductile foods significantly slower than non-preferred apricots (ANOVA: $F=12.26$, $P=0.001$, $n=438$) (Fig. 3). Similarly, capuchin C chewed preferred dates and prunes significantly slower than non-preferred ductile apricots ($F=70.59$, $P<0.001$; Covariate = trial, $n=452$) (Fig. 3). Thus, both capuchins chew preferred, ductile foods significantly slower than non-preferred apricots.

Scaled peak superficial masseter (SM) and temporalis (T) activity exhibited several significant differences with brittle and ductile food preference (Table 2, Figs 4, 5). These differences were not consistent across animals or foods. Across muscles, the balancing-side (BS) superficial masseter (BSM) showed significantly larger peaks in the non-preferred (NP) food compared to the preferred (P) food in three of four comparisons (Table 2). Alternatively, the working-side (WS) temporalis (WST) exhibited significantly larger peaks during chewing of preferred compared to non-preferred foods in three of four comparisons (Table 2). The BST demonstrated no difference with food in three of four comparisons (Table 2).

Looking across animals, capuchin M demonstrated greater scaled muscle recruitment when chewing preferred foods in half of the chewing muscles. For the remaining muscles, this animal showed no difference (3 of 4) or higher recruitment during chewing non-preferred foods (BSM, brittle foods) (Table 2, Figs. 4, 5). Capuchin C showed a more or less inverse pattern where muscle peaks were significantly larger during chewing of non-preferred foods in five muscles. The remaining three were either not different (2 of 3) or significantly larger during chewing of preferred foods (WST, brittle foods) (Table 2, Figs. 4, 5). Given that mechanical properties are relatively similar within these food groups, these results suggest that preference likely impacts oral processing, but the patterns are not consistent across the two individuals.

Discussion

Food preference and oral processing

The two capuchins exhibited clear food preferences that were similar, but not identical. This result corresponds to previous work on capuchins (Visalberghi et al., 2003) and other non-human primates (Hladik and Simmen, 1996; Simmen and Hladik, 1998; Remis, 2002; Hladik et al., 2003) demonstrating behavioral preferences for foods across primates. Unfortunately, we do not know what factors (e.g., sugar content, energy content, learning) influenced food preference in these capuchins (but see Visalberghi et al., 2003). Our contribution suggests that food preference may have some influence on oral processing in primates. This relationship between food preference and oral processing is clearly complex and may be specific to individuals. It may also reflect innate behaviors characteristic of the species, such as aversions to certain compounds, and/or learned preferences specific to individuals. We openly acknowledge multiple potential confounding factors as this is a very preliminary analysis on only two individuals, but our findings justify further testing of the hypothesis that food preference impacts oral processing in primates. The bottom line is that our results provide enough evidence to explore this question further in a more robust study.

We know little about how food preference impacts oral processing. While human studies have demonstrated effects of personality (Rey et al., 2007) and emotions (Diess et al., 2009) on muscle EMG during feeding, we lack a clear understanding of how preference impacts oral processing in humans as well as non-human primates. Horio (2003) demonstrated that disliked solutions tended to elicit greater response from the chewing muscles compared to pleasant tasting solutions. Neyraud et al. (2005) demonstrated that increasing bitterness (i.e., quinine concentrations) in model gels decreased the number of chewing cycles but increased the total sequence length. In the present study, we found that both animals chewed apricots more quickly than other preferred dried fruits (e.g., dates and prunes). Our physiological

experimental setup allowed these animals to learn that they needed to chew a given food, even a non-preferred one, to receive the next food item more quickly. We speculate animals simply chewed highly non-preferred apricots quickly to get to the next, more preferred food as fast as possible. We analogize this to children quickly eating their vegetables in order to get dessert.

Admittedly, our experimental setup is unlikely to realistically replicate wild primate behaviors as free-ranging animals might choose preferred foods first (just as children might eat dessert first if left unattended). However, we must also point out the numerous additional factors in the wild including travel and foraging costs, predation risks, and opportunistic feeding events that may dictate animals choosing non-preferred foods in natural settings. Moving forward, we advocate a combination of semi-realistic laboratory studies that allow manipulation of one or a few of the variables that primates face in the wild in conjunction with ecophysiological studies that examine the oral processing of foods in natural environments. Both laboratory and natural studies could use telemetered EMG equipment that would allow animals more behavioral freedom and reduce the impacts of anesthesia while still capturing oral processing parameters (Williams et al., 2008). Identifying how different potential behavioral strategies interact with oral processing is important for understanding how preference impacts feeding physiology in primates.

We did observe individual differences in oral processing of preferred and non-preferred foods. The tendency for chewing speed to increase with trial number during an experiment in capuchin C (Fig. 2) is likely related to individual differences in the behavioral effects of anesthesia on these two lab primates (Fig. 1) (Thompson et al., 2011). Capuchin C and M differed in how quickly they consumed preferred versus non-preferred brittle foods (Fig. 2). These two individual also demonstrated different levels of muscle recruitment when consuming preferred versus non-preferred foods. Even when they showed similar patterns of consuming non-preferred apricots significantly faster than dates and prunes, their muscle recruitment patterns differed. Capuchin C elicited greater relative recruitment when chewing apricots,

while capuchin M tended to exhibit similar or relatively more recruitment when chewing preferred fruits (Table 2, Figs. 4, 5). While potentially counter-intuitive, we lack additional information on important factors such as taste sensitivities and levels of food reduction (i.e., particle size) that may highlight alternative behavioral strategies for dealing with non-preferred foods. Future work on the relationship between preference and oral processing would benefit from incorporating these data to assess different behavioral strategies.

It is reasonable to consider the relative influence of preference versus FMPs (and other factors) on oral processing. As an initial assessment, we compared effect sizes (η^2 and partial η^2) from a two-way ANOVA incorporating preferred and non-preferred brittle and ductile foods for each capuchin (Table 3). For all oral processing variables, effect sizes are larger for FMPs compared to preference. This is consistent with our common perception that FMPs play an important role in oral processing. We are careful to point out that our design of choosing highly brittle versus ductile foods may exacerbate this relative difference, but we speculate that this basic result would persist in a more balanced survey of FMPs. Following the general recommendations from Cohen (1988) of small = 0.01, medium=0.06 and large=0.14 effect sizes, we see that FMPs tend to exhibit medium to large effects, while preference and the interaction between preference and FMPs tends to involve primarily smaller effects on oral processing (Table 3). Based on our results, we hypothesize that while preference can have a significant effect on masticatory physiology, it will tend to be less than FMPs across primates.

Potential evolutionary links between food preference and oral processing in humans.

Evidence of food preference in non-human primates indicates an evolutionary basis for food 'liking' in humans beyond preferences that are derived from cultural experience (Hladik and Simmen, 1996; Hladik et al., 2003). The associations between preference and oral processing observed in this preliminary analysis also highlight the possibility that relationships observed between palatability and oral physiology in humans (e.g., Bellisle et al., 2000; Horio,

2003; Neyraud et al., 2005) may be shared with non-human primates and thus based on more than lifetime experiences and societal influences. For example, humans share with primates certain aversions to bitter compounds and preferences for sugars and fats (Hladik & Simmen, 1996). Based on our initial results, we can speculate (somewhat wildly) that foods containing these compounds may be consumed differently by multiple primate species based on these shared aversions and/or preferences. Moreover, this observation raises the interesting possibility that the four mouth behavior groupings identified in American consumers (Jeltema et al., 2014, 2015) may reflect both cultural experiences and predispositions toward certain feeding styles shared with groups of non-human primates. These behaviors likely have clear consequences for oral processing. Future studies determining whether preference and oral processing can be linked in comparable ways across primate species will help us to better understand the evolution and lifetime adaptations of feeding behaviors in humans.

Humans as a primate model for studying preference and oral processing

Given how little we know about how food preference might impact oral processing, humans are a practical model for studying the many potential relationships between food liking and oral physiology. Numerous factors make humans a useful model for more detailed study. Model foods are routinely used in food science research to examine how variation in FMPs impact oral physiology (e.g., Peyron et al., 2002; Foster et al., 2006; Woda et al., 2006). Similarly, we can generate model foods that control FMPs and vary preference (e.g., Neyraud et al., 2005). Humans can provide highly detailed assessments of preference, choice and behavioral response (e.g., Meilgaard et al., 2007). We can also assess how satiety and satiation potentially influence preference and oral processing (e.g., Frecka et al., 2008; Hogenkamp and Schioth, 2013). Humans offer a model that does not require restraint or anesthesia, both of which can influence feeding physiology under laboratory conditions in non-human primates (Thompson et al., 2011). Finally, humans provide the opportunity to examine much larger

sample sizes than most other primates facilitating the study of intraspecific variation in these relationships. Because preference may elicit smaller effect sizes on oral physiology, studying humans offers the necessary control of the experimental setup and ability to address multiple potential confounding factors. We advocate using humans initially to provide a clearer picture of these relationships between preference and oral processing followed by more specific hypothesis testing in non-human primates to explore similarities across taxa. It is difficult to speculate what these similarities may be as we know little about the relationship between preference and oral processing at present. Moreover, these relationships may vary with the species being considered. Initially, we would consider variation in food qualities known to impact preference, such as sweetness, bitterness, amounts of fat, and calorie content, as well as masticatory apparatus morphologies known to influence oral physiology.

Summary

Peter Lucas spearheaded the quantitative assessment of food mechanical properties in primate diets that has blossomed over the past two decades. His efforts included logistical advances in the development and proliferation of the HKU field tester (Darvell et al., 1996, Lucas et al, 2001), theoretical improvements in our understanding of the mechanical properties of primate diets (e.g., Lucas, 2004; Lucas et al., 2009) and comparative assessments relating FMPs to morphological variation in primate teeth (Lucas, 1982, 2004). Recently, Berthaume (2016) called for continued expansion of our methods and toolkit for studying the mechanical properties of primate diets; building on the foundation established by Lucas and colleagues. We support this expansion by arguing for exploration of additional avenues of research related to questions such as food preference and choice as we continue to develop a more complete understanding of how primates feed and the evolutionary basis for our own feeding behaviors.

Acknowledgments

Animal procedures were approved by the Institutional Animal Care and Use Committee of NEOMED. We thank Nayuta Yamashita, Erin Vogel and Barth Wright for the invitation to participate in this issue and the symposium in honor of Peter Lucas. Thanks to Mark Teaford for his patience and diligence in getting this done. Thanks to three reviewers that greatly improved this manuscript. We thank E. Çakır, C. Daubert, E.A. Foegeding, H. Koc., P. Luck, and J. Young for comments and fruitful discussions. Finally, we thank Peter Lucas for introducing us to the wonderful world of food material properties.

Grant support: NSF: BCS-0552285, DBI – 1062332.

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Table 1. Food preference rankings in (A.) capuchin M and (B.) capuchin C for twelve foods routinely fed to monkeys in laboratory physiology studies of feeding.

A. Capuchin M

Food ¹	Total number and (%) selections ²	Pairwise comparison to previous ³
Raisin	51 (93%)	3 of 5
Date	51 (93%)	4 of 5
Prune	45 (82%)	5 of 5
<i>Almond</i>	26 (47%)	2 of 4
Peanut	26 (47%)	3 of 5
Popcorn Kernel	20 (36%)	4 of 5
Apple	19 (35%)	4 of 4
Fig	16 (29%)	3 of 4
Cherry Pit	8 (15%)	1 of 3
<i>Monkey Chow</i>	5 (9%)	1 of 3
Carrot	4 (7%)	0 of 0
Apricot	4 (7%)	-
Did not choose ⁴	55	

¹ For pairwise comparisons, ductile foods are bolded, while brittle foods are italicized.

² Represents the total number of times that a food was chosen from 55 total trials versus the remaining 11 food choices.

³ Indicates the number of times in pairwise comparisons that a food was chosen compared to the food immediately below it in the table. For example, Raisin “3 of 5” indicates that Raisin was chosen over Date in 3 of 5 comparisons.

⁴ Indicates number of trials where animal refused to choose either food in pairwise choice test.

488 (Table 1 cont.)

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490 B. Capuchin C

Food	Total number and (%) selections	Pairwise comparison to previous
<i>Almond</i>	51 (93%)	3 of 5
Date	50 (91%)	4 of 5
Peanut	45 (82%)	4 of 5
Raisin	39 (71%)	3 of 5
Apple	28 (51%)	3 of 5
Fig	27 (49%)	5 of 5
Popcorn Kernel	27 (49%)	5 of 5
Prune	25 (45%)	3 of 5
Carrot	16 (29%)	3 of 5
Cherry Pit	13 (24%)	4 of 5
Apricot	5 (9%)	4 of 5
<i>Monkey Chow</i>	4 (7%)	-

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Table 2. ANOVA comparing oral processing parameters for preferred versus non-preferred foods in (A.) capuchin M and (B.) capuchin C. Brittle and ductile foods comparisons are reported separately for each animal.

A. Capuchin M

Brittle foods

Oral Processing Parameter ¹	N	F-value, P-value	Covariate ²	Directionality ³
Cycle Length	830	59.75, <0.001	.	P < NP
WS superficial masseter	928	43.77, <0.001	.	P > NP
BS superficial masseter	923	4.96, 0.03	.	NP > P
WS temporalis	679	10.15, 0.002	Trial	P > NP
BS temporalis	789	3.61, 0.06	.	.

¹ Cycle length refers to mean-centered chewing cycle length. WS=working (or chewing) side. BS=balancing (or non-chewing) side.

² Trial was used as a covariate in comparisons where animals demonstrated significant covariation between oral processing parameters and trial number throughout an experiment.

³ P=preferred foods. NP=non-preferred foods. For cycle length "<" means chewed more slowly.

Ductile foods

Oral Processing Parameter ¹	N	F-value, P-value	Covariate ²	Directionality ³
Cycle Length	438	12.26, 0.001	.	P < NP
WS superficial masseter	501	1.19, 0.28	.	.
BS superficial masseter	508	7.60, 0.006	.	P > NP
WS temporalis	331	5.69, 0.01	Trial	P > NP
BS temporalis	341	0.024, 0.88	.	.

513 (Table 2 cont.)

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515 B. Capuchin C

516 Brittle foods

Oral Processing Parameter ¹	N	F-value, P-value	Covariate ²	Directionality ³
Cycle Length	640	9.76, 0.002	Trial	NP < P
WS superficial masseter	630	1.63, 0.20	.	.
BS superficial masseter	691	12.43, <0.001	.	NP > P
WS temporalis	678	10.64, <0.001	.	P > NP
BS temporalis	686	0.18, 0.67	.	.

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521 Ductile foods

Oral Processing Parameter ¹	N	F-value, P-value	Covariate ²	Directionality ³
Cycle Length	452	70.59, <0.001	Trial	P < NP
WS superficial masseter	433	40.10, <0.001	.	NP > P
BS superficial masseter	423	30.25, <0.001	.	NP > P
WS temporalis	314	62.26, <0.001	.	NP > P
BS temporalis	305	61.44, <0.001	.	NP > P

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Table 3. Effect sizes¹ from a two-way ANOVA considering the influence of food preference and FMPs on oral processing variables during feeding in **(A.)** capuchin M and **(B.)** capuchin C.

A. Capuchin M

Oral Processing Parameter	Preference ¹		FMP		Preference x FMP ²	
	Eta ²	Partial Eta ²	Eta ²	Partial Eta ²	Eta ²	Partial Eta ²
Cycle Length	0.05	0.05	0.08	0.08	.	.
WS superficial masseter	0.01	0.01	0.06	0.06	0.01	0.01
BS superficial masseter	.	.	0.05	0.05	0.01	0.01
WS temporalis	0.01	0.01	0.08	0.08	.	.
BS temporalis	.	.	0.04	0.04	.	.

¹ Eta² estimates the proportion of total variation in the two-way ANOVA attributable to a variable. Partial Eta² estimates the proportion of explained variation in a variable after accounting for explained variation by other variables in the ANOVA. "." Indicates a non-significant factor in the two-way ANOVA.

² Preference x FMP represents the interaction of food preference and FMPs in the experimental design.

(Table 3 cont.)

B. Capuchin C

Oral Processing Parameter	Preference ¹		FMP		Preference x FMP ²	
	Eta ²	Partial Eta ²	Eta ²	Partial Eta ²	Eta ²	Partial Eta ²
Cycle Length	0.03	0.07	0.06	0.04	0.04	0.04
WS superficial masseter	0.02	0.02	0.19	0.2	0.01	0.01
BS superficial masseter	0.03	0.03	0.20	0.2	.	.
WS temporalis	0.01	0.01	0.04	0.04	0.05	0.05
BS temporalis	0.02	0.02	0.19	0.12	0.02	0.03

Figure captions

Figure 1. Plots of mean-centered chewing cycle length (ms) and trial number for (A.) capuchin M and (B.) capuchin C. Brittle foods are represented by filled symbols while ductile foods are open. Solid line represents LS regression slope for the sample (see text for details). Dotted line is LS regression slope for ductile foods and dashed line is LS regression slope for brittle foods.

Figure 2. Plots of mean-centered chewing cycle length (ms) for preferred almonds and non-preferred monkey chow in (A.) capuchin M and (B.) capuchin C. Both are brittle foods.

Figure 3. Plots of mean-centered chewing cycle length (ms) for preferred dates / prunes versus and non-preferred apricot in (A.) capuchin M and (B.) capuchin C. All are ductile foods.

Figure 4. Radar plots summarizing variation in chewing cycle length and scaled EMG activity for brittle foods in (A.) capuchin M and (B.) capuchin C.

Figure 5. Radar plots summarizing variation in chewing cycle length and scaled EMG activity for ductile foods in (A.) capuchin M and (B.) capuchin C.

1A.

1B.

2A.

2B.

3A.

3B.

4A.

4B.

5A.

5B.