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

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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.

1. Introduction

The pioneering work on food mechanics by Lucas and colleagues (Darvell et al., 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 and 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., Hylander et al., 1987, 2000; Horio and Kawamura, 1989; 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 Heymann, 2010), has a significant influence on feeding behaviors. Texture is perceived by animals and can include auditory cues (e.g., the crispness of chips) and visual textures (e.g.,

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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; Remis, 2002; Hladik et al., 2003; Visalberghi 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 processers 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.

2. Materials and methods

2.1. Subjects

We assessed preference and oral processing in two capuchins (*C. 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.

2.2. Preference

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

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.

Food[a]	Total number and (%) selections[b]	Pairwise comparison to previous[c]
A. Capuchin M		
Raisin	51 (93%)	3 of 5
Date	51 (93%)	4 of 5
Prune	45 (82%)	5 of 5
Almond	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
Monkey Chow	5 (9%)	1 of 3
Carrot	4 (7%)	0 of 0
Apricot	4 (7%)	–
Did not choose[d]	55	
Food[a]	Total number and (%) selections[b]	Pairwise comparison to previous[c]
B. Capuchin C		
Almond	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
Monkey Chow	4 (7%)	–

[a] For pairwise comparisons, ductile foods are bolded, while brittle foods are italicized.

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

[c] 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.

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

2.3. Jaw-muscle electromyography

Procedures for constructing and implanting electrodes, as well as collecting EMG data, follow Hylander et al. (2000). Prior to inserting electrodes, we sedated each animal with a combination of medetomidine (0.06 mg/kg) and ketamine (7.0 mg/kg) and seated it in a restraint chair that allowed free head and neck movement. Animals 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 (100–3000 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 ($n = 3274$ chewing cycles). EMG experiments were conducted separately from preference testing.

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[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).