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Great apes prefer cooked food

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ABSTRACT

The cooking hypothesis proposes that a diet of cooked food was responsible for diverse morphological and behavioral changes in human evolution. However, it does not predict whether a preference for cooked food evolved before or after the control of fire. This question is important because the greater the preference shown by a raw-food-eating hominid for the properties present in cooked food, the more easily cooking should have been adopted following the control of fire. Here we use great apes to model food preferences by Paleolithic hominids. We conducted preference tests with various plant and animal foods to determine whether great apes prefer food items raw or cooked. We found that several populations of captive apes tended to prefer their food cooked, though with important exceptions. These results suggest that Paleolithic hominids would likewise have spontaneously preferred cooked food to raw, exapting a pre-existing preference for high-quality, easily chewed foods onto these cooked items. The results, therefore, challenge the hypothesis that the control of fire preceded cooking by a significant period.

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Introduction

The advent of cooking, whether it occurred at the origin of *Homo erectus* or during the Middle Paleolithic, has been hypothesized to have had diverse effects on human physiology and behavior (Coon, 1962; Brace et al., 1987; Wrangham et al., 1999; Wrangham and Conklin-Brittain, 2003; Lucas et al., 2006; Wrangham, 2006). Because cooking reduces food toughness and, thus, would have allowed easier chewing and digestion, a diet of cooked food appears to have contributed to the reduction of tooth size and gut size in hominids (Aiello and Wheeler, 1995; Lucas, 2004). Small guts probably explain why modern humans fare poorly on raw diets (Koebnick et al., 1999) and why no human societies live without cooking (Wrangham and Conklin-Brittain, 2003).

Such indications of biological adaptation to cooking raise the possibility that a preference for eating cooked food is an adaptation rather than an exaptation (i.e., that the preference for cooked food evolved subsequent to the adoption of cooked diets). If so, the problem of how cooking arose is relatively complex because cooking would not necessarily have been adopted quickly after the control of fire. As Stahl (1989: 19) suggested, "use of controlled fire

as a source of warmth may have preceded systematic use of fire in food preparation by thousands or hundreds of thousands of years." Similarly, Bellomo (1994) proposed that when fire was first controlled it was used for heat, light, and defense against predators but not for cooking.

Alternatively, cooked food may have properties that hominoid primates would find desirable even without any evolutionary exposure to cooking. If so, the control of fire would be expected to lead rapidly to cooking, as often implied or suggested (e.g., Oakley, 1963; Clark and Harris, 1985; Brace, 1995; Rolland, 2004; Wrangham, 2006).

No data are currently available to directly distinguish between these hypotheses, but human systems for food perception appear to be generally similar to those in other mammals, including primates (Dominy et al., 2001; Hladik et al., 2003). As such, the findings that rats have been shown to prefer cooked to raw starch (Ramirez, 1992) and cats prefer cooked to raw meat, provided they are familiar with cooked meat (Bradshaw et al., 2000), would suggest that this preference may have been conserved in primates. Yet no past work has investigated this question specifically.

What has been shown is that both nonhuman primates and other animals tend to prefer properties that are produced by cooking. Numerous species prefer foods that are higher in sugar, and cooking raises sugar availability in the mouth by increasing the susceptibility of starch to amylase degradation (Svihus et al., 2005; Tester et al., 2006). Apes in captivity have also been shown to finely discriminate the levels of sugar, in addition to tannins and salt in various foods or aqueous solutions (Hladik and Simmen, 1996;

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Laska et al., 1999; Hladik et al., 2003; Simmen and Charlot, 2003). In the wild as well, food choices of nonhuman primates, including apes, are well-predicted by their sugar or tannin contents, suggesting that individuals might be sensitive to these properties of a food if they were changed by cooking (Leighton, 1993; Conklin-Brittain et al., 1998; Wrangham et al., 1998). Further, cooking increases the availability of glutamate, responsible for the umami taste preference (Sasaki et al., 2007), and umami taste receptors are found widely in invertebrates and vertebrates (Bellisle, 1999). Finally, some of the textural properties to which monkeys respond are the same as those used by humans, such as viscosity, temperature, fat content, and grittiness. Perception of textural properties has in some cases been shown to be mediated in humans and nonhuman primates via similar neural mechanisms (Kadohisa et al., 2004, 2005; Rolls, 2005).

Such evidence indicates that the mechanisms of human food perception are fundamentally similar to those in other primates. Nevertheless, species preferences for any given food are unpredictable (Hladik and Simmen, 1996; Dominy et al., 2001; Hladik et al., 2003). It is, therefore, not known whether the chemical and textural changes induced by cooking would have caused Paleolithic hominids to show increased or decreased preference. However, great apes offer an opportunity to assess whether hominoids have a tendency to spontaneously prefer cooked or raw foods.

Accordingly, in this paper we report on experiments designed to establish whether great ages have an inherent preference for raw or cooked food. We tested apes' preferences by providing the individual being tested with a choice between a raw and a cooked option, then measuring how many times it picked each item. We used three different categories of food to assess apes' preferences: tubers, meat, and fruit. Each individual food might have a different prediction based on the properties of that food which are altered by cooking, thus using this variety of items allowed us to gain some insight into what factors might be influencing subjects' selectivity. In addition to testing general taste preferences in different cooked and raw foods, in experiment 2 we also tested a few hypotheses of why subjects might prefer cooked food. We did so by manipulating the textural properties of the foods in this experiment, juxtaposing the potential taste and tactile changes caused by cooking to attempt to discern what factors would be selected by subjects in a potential preference for cooked food.

Experiment 1: do apes prefer cooked tubers?

In this experiment, we investigated chimpanzees' preferences for cooked versus raw tubers. Tubers are an important class of food for many hunter-gatherers and have likely been significant during human evolution (O'Connell et al., 1999; Laden and Wrangham, 2005: Perry et al., 2007). They are also a category of food where the items are significantly changed in both nutritional and textural quality by cooking (Wandsnider, 1997; Wrangham et al., 1999; Laden and Wrangham, 2005). Tubers are often improved nutritionally by being cooked, since heat gelatinizes starch granules that may otherwise be incompletely digested (Ayankunbi et al., 1991; Kingman and Englyst, 1994; Tester and Sommerville, 2000; Smith et al., 2001; Lucas, 2004). Though chimpanzees in the wild occasionally eat raw tubers (Lanjouw, 2002; Hernandez-Aguilar et al., 2007), tubers are generally not elements of the chimpanzee diet. They therefore represent a relatively unfamiliar type of food for chimpanzees, for which a strong bias towards the raw or cooked items is unlikely to have been selected. The subjects in this experiment had previously tasted our test items-carrots, sweet potatoes, and white potatoes—in both their cooked and raw forms, reducing the possibility that simple fear of novelty might shift preferences away from the cooked items.

Methods

Fourteen chimpanzees (for age and sex, see Table 1) were subjects for this experiment and were housed at the field station at the Yerkes Regional Primate Center in Atlanta, Georgia, USA, when they were tested. The fourteen chimpanzees had various rearing histories, with two individuals (Peony and Ericka) raised in a human family as young infants. At Yerkes all subjects were fed on a diet of monkey chow and various fruits and vegetables provided throughout each day. In the past, all of the chimpanzees had been fed various cooked foods, including the ones they were tested with in the current study. Water was available *ad libitum* during testing. Tubers were sliced across their diameter and baked in the oven at approximately 245 degrees Celsius (°C) until they were soft/edible to a human. All items in this and the subsequent experiments were at room temperature when presented.

Subjects were brought one at a time into a testing room. Each individual was presented with one food preference test consisting of five trials per day. In their first session (on the first test day), subjects were given a choice between cooked and uncooked sweet potato (*Ipomoea batatas*), then in their second session a choice between cooked and uncooked white potato (*Solanum tuberosum*), and finally in their third session cooked and uncooked carrots (*Daucus carota sativus*). Before each testing session the individual was given an introduction in which they were presented with two pieces of uncooked food and two pieces of cooked food of approximately equal size (approximately 2.5 cm diameter slices of carrot and 6.5 cm diameter slices of potato). After the subject finished eating these pieces of food the test session began.

The experimenter held a cooked piece of food in one hand and an uncooked piece of food in the other so that the subject could look, smell, and/or touch both pieces of food (the food pieces were 10–15 cm apart from each other). Once the subject had inspected the food the experimenter then slowly moved her hands out of the subject's reach while also moving them apart and stopped when the food pieces were 50–60 cm apart from each other. Once the food pieces were separated by this distance, they were moved back within reach of the subject. The subject was then allowed to touch one of the two food pieces, and was given the food piece he/she first touched. This procedure was repeated five times for each subject in each session while the position of each food type was alternated each trial and the position presented in the first trial was counterbalanced across subjects. Subjects' choices were scored live by the experimenter.

Table 1Number of choices for cooked items in experiment 1^a

Subject	Sex	Age	Carrot	White potato	Sweet potato	All cooked
Erika	F	26	5	5	2	12
Barbara	F	26	1	5	5	11
Jesse	F	17	5	5	4	14
Sonia	F	39	5	5	5	15
Rita	F	12	3	0	5	8
Borie	F	35	5	1	4	10
Anya	F	19	0	0	3	3
Kate	F	10	5	3	5	13
Peony	F	31	4	4	5	13
Kevin	M	9	5	0	3	8
Phinneus	M	33	1	5	5	11
Travis	M	11	3	0	5	8
Amos	M	22	5	5	3	13
Bjorn	M	11	5	0	5	10
Mean			3.7	2.7	4.2	10.6

^a The number of times each chimpanzee in experiment 1 chose to eat the cooked food when offered a choice between cooked and uncooked carrot, white potato, and sweet potato in five test trials per food type. Scores in **bold** represent those that differ significantly from chance (p < 0.05, binomial probability, one-tailed).

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