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Endowment Effects in Gorillas (*Gorilla gorilla*)

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Reports of endowment effects in nonhuman primates have received considerable attention in the comparative literature in recent years. However, little is known about the mechanisms underlying these effects. Continuing to explore endowment effects across different species of primate may reveal subtle differences in behavior that can help formulate specific hypotheses about the relevant mechanisms and the social and ecological factors that have shaped them. In this study, we use a paradigm that has previously been used to test chimpanzees (*Pan troglodytes*) and orangutans (*Pongo spp.*) to explore whether western lowland gorillas (*Gorilla gorilla*) exhibit comparable endowment effects. We find that gorillas exhibit endowment effects when in possession of food, but not nonfood, items, and that they show a statistically stronger effect than chimpanzees but not orangutans. These findings are consistent with the hypothesis that mechanisms for endowment effects in primates may be related to inhibitory control or risk aversion.

Keywords: endowment effect, cognitive biases, nonhuman primates, gorillas

Standard neoclassical economic theory assumes that decision-making agents make rational choices in order to maximize benefits. However, it has long been recognized that humans often fail to behave in the manner predicted by expected utility theory. Instead, people's decision-making processes seem to be influenced by a suite of cognitive biases that are inconsistent with more traditional mathematical models of optimization (Kahneman & Tversky, 1979). To gain insights into the proximate and ultimate factors that have shaped humans' decision-making processes, comparative researchers have begun to explore whether some cognitive biases are shared with other primate species.

One cognitive bias that has received considerable attention in both the human and nonhuman literatures is the endowment effect—the phenomenon by which individuals tend to value an object in their possession more than that same object just prior to possession (Kahneman, Knetsch, & Thaler, 1991). Intriguingly, recent evidence indicates that several other species of primate, including bonobos (*Pan paniscus*), capuchins (*Cebus apella),* chimpanzees (*Pan troglodytes*), and orangutans (*Pongo spp.*), also behave in ways consistent with endowment effects in some contexts (Brosnan et al., 2007; Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012; Flemming, Jones, Mayo, Stoinski, & Brosnan, 2012; Kanngiesser, Santos, Hood, & Call, 2011; Lakshminaryanan, Chen, & Santos, 2008). Specifically, studies have demonstrated that individual members of these species generally maintain possession of endowed foods rather than exchange them for other, preferred foods. However, whereas humans exhibit endowment effects in a wide variety of situations and with many different objects (reviewed in Jones & Brosnan, 2008), all of the work in nonhuman primates suggests that the effect is specific to food possession and acquisition (Brosnan et al., 2007, 2012; Flemming et al., 2012; Kanngiesser et al., 2011).

Although this recent suite of comparative studies has provided evidence that endowment effects are not unique to humans, little is known about the processes underlying these effects in other species. Continuing to explore endowment effects across different species of primate may reveal subtle differences in behavior that can help formulate specific hypotheses about the relevant mechanisms and the social and ecological factors that have shaped them. Analyses that directly compare the performance of different species on identical tasks are likely to be particularly valuable. Therefore, in this study we utilize a paradigm that has previously been used to explore endowment effects in chimpanzees (Brosnan et al., 2007) and orangutans (Flemming et al., 2012) to test whether western lowland gorillas (*Gorilla gorilla*) also exhibit endowment effects for food but not nonfood items and compare our results to those with the other two ape species. Although a recent study by

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All experiments comply with animal care and safety laws and were approved by Zoo Atlanta's scientific review board as well as by Georgia State University's Institutional Animal Care and Use Committee. Special thanks to the Zoo Atlanta primate staff for their assistance in running this study.

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Kanngiesser et al. (2011) did investigate endowment effects in all four species of great ape, only two gorillas were included in the study. Thus, this is the first study to include an adequate number of gorillas to examine the prevalence of the effect. In addition, we test whether gorillas' performance differs depending upon whether food items are a routine part of the gorillas' diet (referred to as low-value foods) or are foods that the gorillas receive very rarely (referred to as high-value foods).

Method

Subjects

We tested nine western lowland gorillas (*Gorilla gorilla*) living at Zoo Atlanta, Atlanta, GA. Subjects were fed several times daily on a diet of prepared chow, fruits, vegetables, and other enrichment foods and had ad libitum access to water. Prior to testing, all subjects were trained to exchange nonfood items for food items through the mesh caging that separated them from the experimenter. To confirm competency with the exchange procedure, subjects participated in a single session of 10 trials in which they were required to exchange a piece of PVC tubing for a small piece of apple. All subjects passed this initial test with 100% compliance.

Endowed Items

Three different pairs of items were used: high-value foods, low-value foods, and nonfoods. High-value foods included a 16-cm length PVC tube filled with peanut butter (PB) and a fruit-flavored popsicle. Low-value foods included 16-cm pieces of carrot and celery. A rubber bone and a rope toy were used as the nonfood items. The high-value foods and the nonfood items were similar to those used in Brosnan et al. (2007) and Flemming et al. (2012). These previous studies did not include low-value foods. Subjects' familiarity with the two nonfood items was not known, so each subject was given the opportunity to examine and play with the bone and the rope toy on separate days prior to testing. Two gorillas were reluctant to accept the rope and were excluded from all trials involving nonfood items. Note that we use *endowed* throughout the manuscript merely as shorthand for the item initially given to the subject.

Procedure

Subjects participated in three test sessions for each pair of items: one *choice test* and two *endowment tests*. In *choice test sessions*, the two items were presented either in the experimenter's hands (approximately 30-cm apart) or on a 66 × 28-cm polycarbonate panel placed in front of the subject. Subjects were then allowed to choose which item they received by gesturing toward the desired item with their hand or mouth. The item that the subject selected was immediately given to the subject. The location of each item (i.e., right or left side) was counterbalanced. In *endowment test sessions*, subjects were initially shown both items, one in each of the experimenter's hands. The item in the experimenter's right hand was then passed to the subject. Immediately after, the experimenter held out her right hand with the alternative item visible in her left hand, indicating the possibility to exchange the endowed item for the alternative item. Subjects were not allowed to make an exchange if they took more than one bite/lick of a food item and had up to 60 seconds to exchange nonfood items. Subjects completed each session for a given pair of items on different days, and the order in which the pairs were presented and the order of the three test sessions was counterbalanced.

Following test sessions, subjects completed a series of three different controls. Four *choice control sessions* were conducted per subject to assess the stability of each subject's food preferences. The procedure in these sessions was identical to that used in choice test sessions, with the exception that each session consisted of four trials: two involving the high-value food items and two involving the low-value food items. The order in which the pairs of items were presented and the location of each item was counterbalanced across subjects.

Each subject next participated in an *exchange control session* designed to test the possibility that subjects found the exchange procedure inherently rewarding. This session consisted of six different trials, one for each item (except for those subjects that did not participate in nonfood trials, in which case a session consisted of only the four food trials). The procedure in this session was identical to that used in endowment test sessions, with the exception that subjects were presented with two of the same items (i.e., two popsicles, two ropes, etc.) and given the opportunity to exchange one of the items for the other, identical item.

Last, each subject participated in one or more *food control sessions*. This control was designed to test whether subjects were willing to give up the test food items in some situations (specifically when they were being offered a significantly preferred food) and again utilized the same general procedure as in endowment test sessions. Each of these sessions consisted of a maximum of eight trials: four in which the subject had the opportunity to exchange an endowed popsicle for a highly desirable food item and four in which the subject had the opportunity to exchange an endowed carrot for a highly desirable food item. A banana served as the food item offered in exchange for the endowed item during the first food control session [a banana was also used in the equivalent control condition in Brosnan et al. (2007) and Flemming et al. (2012)]. Once a subject completed an exchange with the popsicle or the carrot, testing with that food item concluded and no additional trials were conducted. Any subject that did not exchange the popsicle and/or carrot for the banana participated in additional food control sessions, in which the subject was offered the opportunity to exchange a popsicle and/or carrot for variety of other desirable food items (e.g., sugarcane, flavored gelatin, etc.). Each of these desirable food items was offered in only one session, with the exception of the banana, which was offered in two separate sessions. If a subject had still not traded either of the endowed food items after a maximum of 11 food control sessions had been conducted (using 10 different desirable food items), then that subject participated in one additional session consisting of four trials. In each trial, the subject was endowed with a yellow squash (a food item that the gorillas consume but that is relatively undesirable) and was given the opportunity to exchange it for a banana. The purpose of this final session was to see if subjects who had not previously exchanged food items might be willing to do so if the endowed item was extremely low-value.

Analysis

All test sessions were videotaped. Subjects' behavior was coded during test sessions as well as from all videos by a single experimenter. A second experimenter coded approximately 60% of all sessions. Interobserver agreement was excellent (Cohen's $\kappa >$ .99). McNemar's tests were used to assess whether the number of subjects that selected each item in the initial choice test differed significantly from the number of subjects that maintained possession of that same item in the endowment test. To compare subjects' willingness in endowment tests to exchange endowed high-value foods, low-value foods, and nonfood items for the alternative item, every subject was assigned a score based on the total number of exchanges made per pair. A minimum score of zero was assigned when the subject never exchanged the endowed item for the alternative item and a maximum score of two was assigned when the subject always exchanged the endowed item for the alternative item. Scores between pairs were compared using Wilcoxon's matched-pairs signed-ranks tests with a Bonferonni corrected alpha level of .017. To test whether performance differed across species, pairwise Fisher's exact tests with a Bonferonni corrected alpha level of .017 were used to compare the proportion of gorillas, chimpanzees (Brosnan et al., 2007), and orangutans (Flemming et al., 2012) that traded at least one endowed item for the alternative item for both the high-value food pair and nonfood pair. All statistical tests are two-tailed.

Results

Results from McNemar's tests comparing the number of subjects that selected each item within a pair in choice tests with the number of subjects that maintained possession of that item in endowment tests are summarized in Table 1. For all food items, the number of subjects that maintained possession of the item when it was endowed was greater than the number of subjects that chose that item, and this difference was significant in the case of the popsicle ($p = .014$) and the celery ($p = .008$). In fact, 89% of subjects (i.e., all but one) never exchange an endowed food item. Turning to the two nonfood items, the number of subjects that maintained possession of each endowed item was actually less than the number of subjects that chose that item. This difference was significant in the case of the rope ($p = .046$). Only a single subject ever maintained possession of an endowed nonfood item. We found no significant difference in subjects' willingness to exchange the two pairs of food items ($Z = -1.00$, $n = 9$, $p = .317$), but we did find significant differences between both of the food and nonfood pairs (high-value foods: $Z = -2.53$, $n = 7$, $p = .011$; low-value foods: $Z = -2.45$, $n = 7$, $p = .014$).

The percent of time that subjects chose between the two options in a given food pair remained relatively stable between the choice test session ($n = 9$ total trials per pair collapsed across all subjects) and choice control sessions ($n = 72$ total trials per pair collapsed across all subjects): PB: 67% versus 60%; popsicle: 33% versus 40%; carrot: 89% versus 85%; celery: 11% versus 15%. Looking at the stability of each individual's preferences, we found that for the high-value food items, seven subjects selected the same item that they had selected in the choice test on the majority of the eight trials in choice control sessions ($M = 6.57$, 95% CI [5.39, 7.75]). In the low-value food condition, again, seven subjects selected the same item that they had selected in the choice test on the majority of the eight trials in choice control sessions ($M = 7.14$, 95% CI [6.15, 8.13]).

In the exchange control, no subject exchanged any of the food items for another identical item; however, all subjects traded both nonfood items for the identical item. Subjects' behavior in food control sessions was variable. Five subjects exchanged both an endowed popsicle and an endowed carrot for a desirable food item, one subject only exchanged a carrot for a desirable food item, one subject only exchanged a yellow squash for a desirable food item, and two subjects never exchanged any endowed food. The six subjects that exchanged at least one of the test food items took an average of 4.17 (95% CI [0.45, 7.89]) sessions to make their first food-for-food exchange, although two subjects did exchange both the popsicle and the carrot for a banana at the first opportunity. The majority (approximately 67%) of all food-for-food exchanges occurred on the first trial using a particular food combination and fewer than 17% of exchanges occurred after the second trial.

A comparison of the performance of gorillas ($n = 9$), chimpanzees ($n = 33$) and orangutans ($n = 7$) when endowed with high-value food items revealed that a significantly larger proportion of chimpanzees exchanged items as compared to gorillas ($p =$

Table 1
Results of McNemar's Tests Comparing the Number of Gorillas That Chose Each Item in the Choice Test With the Number of Gorillas That Maintained Possession of That Item in the Endowment Test

Item	% Chose in choice test[a]	% Kept in endowment test[a]	$\chi 2(1)$-Value	*P*-Value	95% CI[b]	
					Lower limit	Upper limit
High-value foods						
Popsicle	33	100	6.0	.014	−87.94%	−23.41%
PB	67	100	3.0	.083	−64.58%	3.37%
Low-value foods						
Carrot	89	100	1.0	.317	−43.50%	20.16%
Celery	11	89	7.0	.008	−90.68%	−31.97%
Nonfoods						
Bone	29	0	2.0	.157	−12.29%	64.11%
Rope	71	14	4.0	.046	5.82%	80.62%

[a] For all food items, $n = 9$; for all nonfood items, $n = 7$. [b] 95% confidence intervals are presented for the difference in the proportion of subjects that selected an item during choice tests compared to the number of subjects that retained possession of that item in endowment tests. Negative values indicate that a greater proportion of subjects maintained possession of the item in endowment tests than chose that item in choice tests.

.002). No other species differences were found (all *p*s > .17; Figure 1). There were also no significant differences in the proportion of subjects within each species that traded nonfood items (gorillas: $n = 7$; chimpanzees: $n = 31$, orangutans: $n = 7$; all *p*s > .08; Figure 1).

Discussion

Results of this study provide evidence that, like other ape species, gorillas are reluctant to exchange a food item in their possession for another, preferred item. The proportion of subjects that selected each food item in choice tests was always less than the proportion of subjects that maintained possession of that item when it was given to them in endowment tests. In fact, only a single subject ever exchanged an endowed food item for the alternative item in a pair. We also found that subjects' behavior did not differ depending upon whether pairs of food items were high-value or low-value, suggesting that endowment effects in gorillas may be equally strong for foods that are a routine part of their diet as for foods that are provided only rarely. In contrast to the gorillas' behavior with food items, and consistent with the behavior of other ape species, gorillas were perfectly willing to exchange endowed nonfood items for alternative items.

Although results follow the same general pattern that has been found in other studies, some potential differences were also noted. When we directly compared the proportion of gorillas versus chimpanzees that exchanged at least one high-value food for the alterative high-value food during endowment tests, we found that significantly more chimpanzees did so (approximately 57% of chimpanzees vs. 0% of gorillas). The proportion of orangutans that traded at least one of the food items (approximately 29%) did not differ significantly from either of the other species tested. Gorillas' performance also differed from that of other apes species in food control sessions. Whereas all 31 chimpanzees and all but one of seven orangutans exchanged a popsicle for a banana in the very first session, only two gorillas did so. This may reflect differences in the magnitude of endowment effects across species. Alternately, it is possible that although species showed the same order of food preferences, the magnitude of preference varied between species. That is, the gorillas in our study may have liked bananas less (or popsicles more) than did the chimpanzees and orangutans in the previous studies.

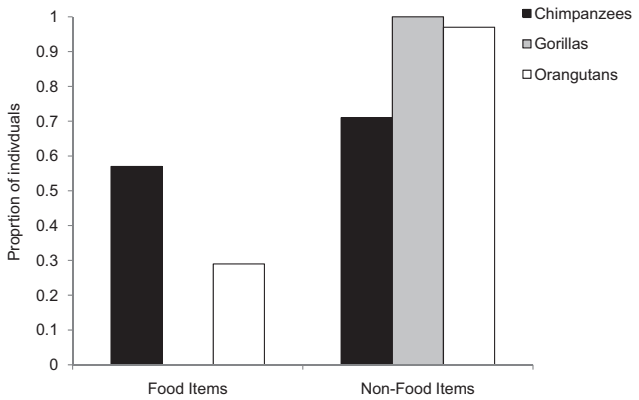

Figure 1. Proportion of chimpanzees (Brosnan et al., 2007), gorillas (current study), and orangutans (Flemming et al., 2012) that traded at least one item for an alternative item during endowment test sessions for food and nonfood pairs. Data from the low-value food pair in this study are not included because no equivalent pair was included in the other two studies.

The interspecies differences reported in this study hint at possible mechanisms underlying endowment effects in nonhuman primates. Specifically, these results align well with Kanngiesser and colleagues' (2011) suggestion that primates may fail to exchange foods in their possession for preferred foods because they have difficulty inhibiting consumption of endowed food items. A previous study found that chimpanzees significantly outperformed gorillas in tasks involving inhibitory control but that there were no significant differences between chimpanzees and orangutans or between gorillas and orangutans (though gorillas did generally perform poorly compared to other ape species; Amici, Aureli, & Call, 2008). Thus, interspecies differences in endowment effects directly parallel interspecies differences reported on inhibitory control tasks. Variation in species' willingness to exchange food items may also be related to variation in species' willingness to engage in risky behaviors, particularly if exchanging rather than retaining possession of endowed items is perceived as the riskier option by subjects. A recent study exploring risk-taking strategies in great apes found that chimpanzees and orangutans were more risk seeking than gorillas and bonobos in some contexts (Haun, Nawroth, & Call, 2011), and so we might expect gorillas and bonobos to exchange food items infrequently. Although the results of our study are largely consistent with this prediction, we note that Kanngiesser et al. (2011) did not find any species differences in endowment effects between orangutans and bonobos.

Given the relatively small sample sizes included in our analyses, additional studies are needed to assess the mechanisms underlying endowment effects. Future studies could investigate whether individuals who perform better on tasks requiring inhibitory control or who are more risk seeking are more willing to exchange endowed food items for preferred food items than are conspecifics. In addition, we note that the above explanations provide hypotheses about the cognitive mechanisms that underlie the behavior, but do not provide insight into its evolutionary function. Additional comparative work studying both primate and nonprimate species will be needed to better understand the function and evolutionary history of endowment effects.

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