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Report

Endowment Effects in Chimpanzees

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Summary

Human behavior is not always consistent with standard rational choice predictions. Apparent deviations from rational choice predictions provide a promising arena for the merger of economics and biology [1–6]. Although little is known about the extent to which other species exhibit these seemingly irrational patterns [7–9], similarities across species would suggest a common evolutionary root to the phenomena. The present study investigated whether chimpanzees exhibit an endowment effect, a seemingly paradoxical behavior in which humans tend to value a good they have just come to possess more than they would have only a moment before [10–13]. We show the first evidence that chimpanzees do exhibit an endowment effect, by favoring items they just received more than their preferred items that could be acquired through exchange. Moreover, the effect is stronger for food than for less evolutionarily salient objects, perhaps because of historically greater risks associated with keeping a valuable item versus attempting to exchange it for another [14, 15]. These findings suggest that many seeming deviations from rational choice predictions may be common to humans and chimpanzees and that the evaluation of these through a lens of evolutionary relevance may yield further insights in humans and other species.

Results and Discussion

The endowment effect (sometimes called the "status quo bias" [16]) describes the tendency to value a good that one has just come to possess significantly more than the maximum price one would have paid to acquire it a moment ago [10–13]. The precise cause and extent of the effect are much debated [17–20]; however, many studies suggest that ownership (endowment) alone instantaneously increases humans' subjective value of a good [10–13, 21–23]. This effect of ownership seems illogical because the good has not changed and no new information or experience can yet have been acquired. The pricing skew that the endowment effect creates has significance beyond paradox because it can impede efficient allocation and exchange of goods and tradable rights [15, 24]. From an evolutionary perspective, however, some inclination to value goods one possessed over goods one might obtain through exchange may have been adaptive. Exchanges are fraught with the potential for defection, particularly in the absence of reliable property rights and third-party enforcement mechanisms (such as the legal rules and institutions of modern humans). In the present study, we investigate whether the endowment effect is present in chimpanzees and how the evolutionary salience of the objects affects the response.

This study was modified from Knetsch's study [12], which suggested that humans often prefer to maintain an object they have just acquired over one they could achieve through exchange. Subjects were given a coffee mug or chocolate bar for agreeing to complete a questionnaire, then, after completion, were offered the opportunity to exchange their item for the other. One group was initially endowed with a mug, the second with a chocolate bar, and the third was given a choice between the two (with no opportunity to exchange). Subjects from the former groups showed a stronger tendency to maintain the object in their possession than would be expected on the basis of preferences shown by the third group.

For our study, we used two versions of the paradigm, one with food and one with nonfood items, to test the hypothesis that, in chimpanzees, evolutionarily relevant stimuli may elicit different responses. We used a within-subjects design in which chimpanzees encountered six trials, three for food and three for nonfood. The three trials for each version consisted of (1) a choice between items (between two foods or between two nonfoods) and (2) one trial each in which chimpanzees were given one item (food or nonfood) and allowed to exchange for the other of the same category. An endowment effect could be concluded if there was a stronger tendency to maintain possession of an item than is expected on the basis of their separately expressed preferences.

This design has several advantages. First, it allows for a good comparison between humans [12] and chimpanzees. Second, the exchange methodology has been used successfully in the past for examining complex phenomena in chimpanzees [25, 26]. Finally, our within-subjects design allowed us to test for the endowment effect both at the population (as in Knetsch) and individual levels and thus enabled a more detailed analysis [27].

Subjects were 33 chimpanzees housed at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas M.D. Anderson Cancer Center. Food items were a frozen fruit-juice stick and a PVC pipe filled with peanut butter (PB), both of which

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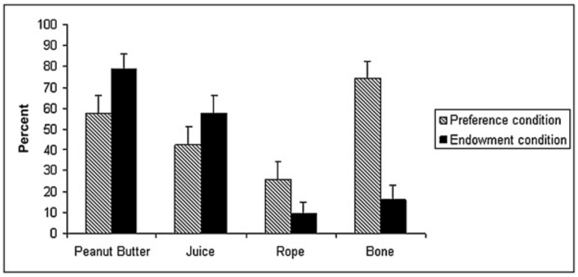

Figure 1. Population-Level Comparisons of Preferences in the Choice and Endowed Conditions

Data are presented as mean + SE. Hatched bars represent the percentage of the population that preferred the object in a choice condition, and solid bars represent the percentage of the population that chose to maintain possession.

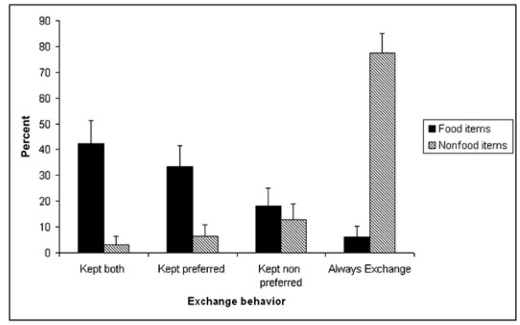

Figure 2. The Behavior of Individuals in the Four Tests

Data are presented as mean + SE. "Kept both" indicates individuals who chose to maintain possession of both foods or both nonfoods rather than exchange; "kept preferred" indicates individuals who chose to maintain possession of their favorite item but exchanged for the other when endowed with their less preferred, "kept nonpreferred" indicates individuals who chose to maintain possession of their nonpreferred item but exchanged for the other when endowed with their preferred item, and "exchanged both" indicates individuals who chose to exchange for the other item in both situations. Solid bars indicate food items and hatched bars indicate nonfood items.

are familiar, favored foods that cannot be rapidly consumed by chimpanzees, diminishing impulse-control problems. Nonfood items were a rubber-bone dog chew toy and a knotted-rope dog toy (hereafter, bone and rope), both of which are made of the same materials as enrichment items to which the chimpanzees have regular access.

To replicate Knetsch [12], we first examined data for the population. As a group, 58% of the chimpanzees preferred PB to juice. However, when endowed with the PB, 79% of the chimpanzees preferred to keep the PB rather than exchange for juice (Figure 1; $\chi^2 = 6.079$, $p = 0.014$); this is approximately 20% more of the population than would be expected from the population-wide preference. Likewise, when endowed with juice (42% preference), 58% of the chimpanzees chose to keep the juice rather than exchange for peanut butter ($\chi^2 = 3.102$, $p = 0.078$), reflecting an endowment effect in approximately 15%. To compare to humans, in Knetsch's study, approximately 33% more people kept their mugs and 46% more kept their chocolate bars than expected given the population preferences under the choice condition.

For nonfoods, subjects showed a preference to exchange the object rather than an endowment effect. The population preference for bone over rope was 74%. However, when endowed with the item, subjects kept the bone only 16% of the time (Figure 1; $\chi^2 = 54.587$, $p < 0.001$) and the rope only 10% of the time ($\chi^2 = 4.212$, $p = 0.040$). Both of these indicate far more exchange of nonfood items than predicted by their separately expressed preferences, indicating that for nonfoods, chimpanzees either lack strong preferences or prefer human interaction over the object.

The previous analysis masks the behavior of individuals. If the endowment effect were present at the individual level, subjects should maintain possession of both the more-preferred and the less-favored item. This was the most common behavior for food items, with 42% of individuals maintaining possession of both foods (Figure 2; $\chi^2 = 9.14$, $p < 0.05$). Thirty-three percent of the subjects showed behavior that matched their preferences, by maintaining possession of the preferred food and exchanging the less-favored food. Seven percent of subjects exchanged in both situations, indicating a preference for interaction. Eighteen percent of individuals behaved inconsistently with their preference under the choice condition, perhaps indicating a weak preference between the items.

For nonfoods, only one subject (3%) maintained possession of both items, indicating an endowment effect. The majority of subjects exchanged in both situations (Figure 2; 77% of subjects, $\chi^2 = 39.41$, $p < 0.05$), perhaps indicating that for less evolutionarily salient objects, subjects are more interested in the interaction than in the items themselves (see below). Six percent of subjects showed exchange behavior consistent with their established preferences, and 13% showed exchange behavior inconsistent with their established preferences.

Finally, we directly compared the individuals' responses in the food and nonfood conditions. Individuals were much more likely to exchange nonfoods than foods ($t = 9.133$, $df = 29$, $p < 0.001$), and no subject exchanged more frequently for foods than nonfoods.

The food rewards were originally chosen to be close in value because large differences in preference would probably result in the favored item being chosen every time, and only a single preference test was run to avoid overexposing the subjects to the commodities. To verify the stability of the chimpanzees' preferences, we ran three additional food choice sessions. Again, 69% of subjects chose PB. Additionally, this preference was extremely consistent; 69% of subjects chose PB in the first of the three sessions, and 67% of subjects chose PB in the first trial of each of the three sessions. This consistency indicates that the single choice in the original study adequately described the population food preferences.

For evaluating whether exchange was due to a preference for interacting with the experimenter, subjects were presented with each of the four items, and exchange was solicited for an identical object. No subject exchanged the PB, and only one subject exchanged the juice. The converse was true with the objects; 82% of subjects (23 of 28) traded a bone for a bone, and 79%

(22 of 28) traded a rope for a rope, compared to 84% of subjects trading a bone for a rope and 90% of subjects trading a rope for a bone in the original exchanges. Thus, in contrast to the result for foods, for toys the interaction with the experimenter is apparently preferred over the object itself.

Finally, to verify that subjects were willing to trade the foods, we offered to trade a small piece of frozen juice for a whole stick. Thirty-six percent (10 of 28) of subjects made this trade. However, the smaller piece of frozen juice was bite sized, thereby enabling immediate consumption, which could preclude an opportunity for subsequent trade. Consequently, we ran a second study with foods that could not be eaten as rapidly, to avoid potential complications from poor impulse control. Subjects could trade a frozen-juice stick (the same size as in previous tests) for a banana (a preferred food) of approximately the same length. Twenty-six of 29 subjects (90%) exchanged on the first presentation, and the remaining three did so on the second trial. Thus, whereas 58% of chimpanzees kept the frozen juice when they were offered a trade for PB, only 10% kept it when they were offered a banana (and none kept it in their second opportunity). This, combined with the sharp difference between exchange behavior for food and nonfood items, supports the conclusion that the frequent failure to exchange a less-favored food for a more-preferred food was an active choice to maintain possession of the food item. This is consistent with human behavior that has been interpreted as an endowment effect [12].

Three features of chimpanzee ecology may help explain the differences in endowment-effect prevalence between foods and nonfoods. The first is that foods have more significant effects on fitness than nonfood items. Second, chimpanzees do not show long-term possession or storage, so items neither accumulate nor have value outside their immediate utility (S.F.B., M. Grady, S.P.L., S.J.S., and M.J. Beran, unpublished data). Third, chimpanzees lack the reliable, institutionalized, third-party bargain-enforcement mechanisms that humans have. This renders each exchange inherently risky because there can be no guarantee that giving up one item will yield another, instead of a total loss. Thus, for chimpanzees, and early humans, there was likely to be a fitness advantage to maintaining possession of some items even in the presence of superior exchange options, thereby making selectively possessive behavior that appears irrational in the moment rational from an evolutionary perspective. Humans in modern times may still exhibit stronger endowment effects in evolutionarily salient situations, a hypothesis that warrants further empirical investigation in light of the puzzlingly varying frequencies and magnitudes in which humans exhibit endowment effects and other seemingly paradoxical behaviors.

As with any evolutionary explanation, it is difficult to fully exclude other possibilities, although several of these do not explain the data as well. For example, this effect cannot be attributed to an inability to delay gratification because chimpanzees can delay gratification for food within their reach for at least 120 s [28], far longer than required in the current study. Moreover, some models of the endowment effect predict that it will be weaker for items that one knows cannot be kept [20]. Although this more deliberative explanation might have played some role in our subjects' responses to toys, socially housed chimpanzees such as these can withhold objects from humans until they are ready to relinquish them. Finally, some attribute of the items may affect behavior. For instance, food items in the wild might increase in value, after preparation for eating, whereas toys may be valuable for novelty and only when new. Yet our subjects exchanged toys for an identical toy, indicating that novelty was not particularly salient. The most obvious explanation is that subjects like to exchange and that food outweighs the utility of the exchange interaction, whereas objects have less utility than the interaction. Yet, this explanation begs the question of why chimpanzees prefer food over objects and interactions in the first place.

Understanding the evolution of widespread behaviors that are often considered economically paradoxical or "irrational" may deepen understanding of their potential functions and thus their patterns in both human and nonhuman species (O.D.J. and S.F.B., unpublished data). Our results suggest that the basis of these asymmetries in exchange behavior is shared by humans and chimpanzees. This in turn indicates that their presence in humans is probably the result of common evolutionary processes rather than, as is often assumed, either cognitive quirks unique to human brains and experience or misunderstandings of experimental instructions (also unique to humans). Further cross-species research on other areas in which humans demonstrate apparently irrational economic behaviors might elucidate the situations in which they are relevant and shed light on the evolutionary history of this class of behaviors. Such research will help to provide a much-needed theoretical foundation for human deviations from standard rational choice predictions.

Experimental Procedures

Subjects were adult chimpanzees drawn from a population of socially housed chimpanzees. No food or water deprivation was done prior to testing, so subject motivation depended on the presence of rare and favored treats. All subjects participated voluntarily and isolated from the rest of their group (for minimization of distractions). No subject received more than one trial per day. Thirty-seven subjects began the experiments, but analyses reflect data from only the individuals that completed all sessions for food or nonfood items. Food items were chosen to be difficult to consume rapidly and easy for chimpanzees to pass through caging (required for exchange). Nonfood items were introduced for this test but were of the same color and materials as other routine enrichment objects.

Prior to the study, all subjects had been trained to exchange objects back to the experimenter for a food reward. During exchange trials, subjects were first shown both objects, then one object was given to the chimpanzee and the other was immediately offered for exchange. Chimpanzees had to return the object they possessed to the experimenter within 120 s (and with no more than a single taste) to obtain the other. Half of subjects began with the three food trials; the other half began with nonfood trials. Otherwise, trials were completed in random order. A forced-choice task elicited subjects' favorite foods [29, 30]. For this, chimpanzees were offered two different rewards and received the one to which they gestured [29].

To compare frequency of exchange in food versus nonfood conditions, subjects who completed all six sessions (n = 30) were given a score, calculated by subtracting the number of exchanges in the food conditions with those in the nonfood conditions. A t test compared these scores to 0, the score if the number of exchanges was the same in both conditions.

Approximately 12 months later, several control experiments were run on 28 of the original subjects, with identical methodology and rewards to the above. Trials were always randomized within a session. Subjects first completed three food-choice sessions, each consisting of four trials in which they had to choose between the two food choices. After this, subjects were given a single session of four trials in which subjects were given an item (frozen juice, peanut butter, rope, and bone) and then allowed to exchange for an identical item. Finally, subjects were given a session in which they could exchange either a medium (3 inch) or small (1.5 inch) piece of frozen juice for a whole juice stick (6 inches). Each option was offered twice. Next, subjects were given a single session in which they were given a whole juice stick and allowed to exchange for a whole banana. If subjects failed to exchange, they were given one additional trial.

All procedures used in the research are in accordance with the Guidelines for the Use of Animals in Research and have been approved by the Institutional Animal Care and Use Committee of UT/MD Anderson Cancer Center.

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