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Original Article

Evolution and the expression of biases: situational value changes the endowment effect in chimpanzees

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Abstract

Cognitive and behavioral biases, which are widespread among humans, have recently been demonstrated in other primates, suggesting a common origin. Here we examine whether the expression of one shared bias, the endowment effect, varies as a function of context. We tested whether objects lacking inherent value elicited a stronger endowment effect (or preference for keeping the object) in a context in which the objects had immediate instrumental value for obtaining valuable resources (food). Chimpanzee subjects had opportunities to trade tools when food was not present, visible but unobtainable, and obtainable using the tools. We found that the endowment effect for these tools existed only when they were immediately useful, showing that the effect varies as a function of context-specific utility. Such context-specific variation suggests that the variation seen in some human biases may trace predictably to behaviors that evolved to maximize gains in specific circumstances.

Keywords: Cognitive biases; Behavioral biases; Endowment effect; Decision-making; Chimpanzee; *Pan troglodytes*; Human evolution

1. Introduction

Cognitive and behavioral biases are widespread among humans. For example, we change our preferences as a function of how choices are framed; we overly discount the future; we fear a loss more than a missed opportunity for equivalent gain; and we ascribe markedly different values to the same item, depending on whether or not we own it (Frederick, Loewenstein, & O'Donoghue, 2002; Kahneman, Knetsch, & Thaler, 1991a; Kahneman, Knetsch, & Thaler, 1991b). Such biases are important to study, as they affect decision-making and render modeling behavior based on the common assumption of rationality quite difficult. Although the roots of these biases are unknown, one possibility is that they are based on evolved tendencies. If this is the case, then these biases may be explicable and predictable, reflecting previously unrecognized patterns (Gigerenzer, 2000; Gigerenzer, Todd, & Group, 1999; Haselton et al., 2009; Haselton & Nettle, 2006; Jones, 2001; Jones & Goldsmith, 2005. See also McKay & Efferson, 2010, for a discussion of the difference between cognitive and behavioral biases, and when that distinction can matter. For our purposes here, the distinction is immaterial.).

There is growing evidence that this is the case. Recent discoveries of such biases in other primates, including the endowment effect (Brosnan et al., 2007), loss aversion (Chen, Lakshminarayanan, & Santos, 2006), and inter-group bias (Mahajan et al., 2011), suggest that some biases persist because of the benefits they once provided (Jones, 2001; Jones & Brosnan, 2008). For instance, capuchin monkeys making decisions in a scenario reminiscent of the Asian Disease problem show behavior very much like that of humans, preferring to minimize risk in the context of loss, but preferring the opposite pattern in the context of gains. Although the study of Chen et al. (2006) did not

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investigate this, the response is unlikely to be due to a simple aversion to ambiguity, as chimpanzees and bonobos are able to distinguish risk and ambiguity (Rosati & Hare, 2010). These are particularly relevant biases, as loss aversion and the endowment effect are presumably linked (Kahneman et al., 1991b).

The exchange-based endowment effect provides a ready lens to test the adaptation hypothesis, both because it has been documented widely, including in other species, and because it is not language based, opening up myriad experimental possibilities, including comparative studies. The endowment effect is the phenomenon by which individuals immediately begin to value what they have just come to possess much more than they valued the same item prior to the moment of possession (Franciosi, Kujal, Michelitsch, Smith, & Deng, 1996; Kahneman, Knetsch, & Thaler, 1990; Kahneman et al., 1991b). The phenomenon is widespread in humans and is seen in other primates that have been tested, including chimpanzees, orangutans, and capuchin monkeys (Brosnan et al., 2007; Flemming, Jones, Stoinski, Mayo, & Brosnan, in review; Lakshminarayanan, Chen, & Santos, 2008).

The underlying causes of this bias are widely debated in the human literature. For example, as Korobkin (2003) explained, some scholars speculate that the effect arises from uncontrolled artifacts of the experimental setting, such as strategic bargaining or unintended, but perceived, signals within the experimental manipulation. Others question whether the effect is caused by the role of personal wealth in valuation processes (such as wealth effects or constraints on liquid resources). Many believe that the effect is a manifestation of "loss aversion" (and its cousins attachment, regret avoidance, and the disutilities of selling; Camerer, 2005). Still others, attempting formal models, argue that buying scenarios create significantly different expectations and reference points than selling scenarios, and that these differences are the root cause of the observed changes in behavior (Koszegi & Rabin, 2006). Plott and Zeiler are among the most vigorous critics of the idea that the observed disjunctions between maximum buying and minimum selling prices (which they argue can be altered by subtle changes in experimental conditions) are in fact related to "endowment" at all (Plott & Zeiler, 2007; Plott & Zeiler, 2005). And, as many have observed (e.g., Jones & Brosnan, 2008; Korobkin, 2003), there is far closer consensus on the existence of an effect than there is on its underlying causes.

One of the critical drivers of this controversy about causes—within economics, behavioral economics, psychology, and law—is the widespread and seemingly unpredictable variation in the effect (Sayman & Onculer, 2005). But if the bias results from evolutionary processes, as the primate studies suggest, rather than simply vagaries of experimental design, then there should be some underlying consistency with respect to the situations in which the effect emerges and when it does not. If this is the case, then an understanding of the underlying causes of this variation could illuminate previously hidden patterns in the human decision-making architecture—not only with respect to the endowment effect, but also with respect to the entire suite of biases.

It is one of these underlying causes that we investigate here. One important feature of the endowment effect is that it appears in the context of exchange. Such interactions are inherently risky, as a willingness to exchange one item for a preferred item possessed by a seemingly willing exchange partner could instead result, through defection of the exchange partner, in the loss of both items. Thus, one reasonable hypothesis is that the effect should be greater in contexts in which the risk of a partner's defection is higher. This risk depends not only on the relationship between partners, but also on the value of the object. Possessors may be unlikely to give up a particularly valuable object, raising the risk of defection. However, while these results do not test this, it seems unlikely that this was an issue given our procedure, in which experimenters reliably exchanged. In addition, and what we examine in the current study, is the value to the individual making the decision whether to exchange. That is, if there is an evolutionary basis to this effect, one would expect manifestations of the effect to vary as a function of immediate usefulness of the object. A specific prediction emerges from this hypothesis: the effect should vary as a function of the instrumental value, or usefulness, of the object at issue to the individual making the decision to exchange (which affects the costs actually incurred from failed exchanges and, hence, the overall risk).

In fact, previous studies of the endowment effect hint at this possibility. The aforementioned study on chimpanzees (Brosnan et al., 2007) was designed to replicate an earlier study of humans by Knetch (1989), which compared one group's preferences for a mug versus a chocolate bar to two other groups' tendency to exchange when endowed with one and given the option to exchange for the other. We hypothesized that subjects would treat food and nonfood items differently, given the extreme salience of food to chimpanzees and the relative lack of interest in nonfood objects (e.g., chimpanzees retain few nonfood items, including tools, in their possession over extended periods; Brosnan, 2011). Thus, we ran two different versions: one using familiar preferred foods and one using familiar toys. We found a strong endowment effect, within the range of human studies, when using foods, but no endowment effect when using nonfoods. In fact, in the latter case, the subjects vastly preferred to trade, perhaps indicating a preference for interaction with the human experimenter over the items themselves. Although we could not rule out confounds such as a general lack of interest in nonfoods, the results nonetheless indicated the possibility that chimpanzees treat food–food exchanges categorically differently from exchanges of nonfoods. Yet that study design did not allow us to test the subtler possibility that endowment effects in chimpanzees' might change for the *same* item (a nonfood) depending on whether the item is situationally useful, for instance, giving the chimpanzees an immediate ability to obtain food. Thus, the current study was designed to test the hypothesis that chimpanzees' behavior would change for the same nonfood item, a tool, depending on whether it could be used to obtain food.

To do this, we followed a similar procedure to test the endowment effect, but did so using the same pair of (nonfood) objects in all conditions. This removed the possibility that an inherent difference between the objects caused any difference in the subjects' responses. These objects were tools that could be used to obtain a specific food (juice or sweetened oatmeal), but neither of which could be used to obtain the other food. These tool pairs were tested in three situations: one in which neither food was available or visible (i.e., the tools could not be used to obtain food), one in which both foods were both visible and available (i.e., the tools were *both* useful), and one in which both foods were visible but not reachable. This latter controlled for the possibility that the very presence of food might change subject preferences, which was particularly important since the tools are secondary reinforcers that might have been treated similarly to the foods they could acquire (Breland & Breland, 1961), even when those foods were not actually accessible.

This design removed a number of confounds. First, as mentioned previously, the fact that the same pair of objects was tested in all three cases removed the possibility that some difference other than the tool's usefulness affected their responses. Second, the fact that neither tool could be used to obtain the other food removed the possibility that they would consider one tool "good enough" for either food and thus be disinclined to exchange. Third, the control situation, in which foods were visible but not available, allowed us to rule out the possibility that it was the presence of foods that caused any response, rather than the usefulness of the objects themselves.

Finally, human studies universally utilize between-subjects designs to compare group-level preferences, obscuring any data on individuals' behavior in such tasks. These data may be very important; an effect at the group level could be due to a few individual's preferences rather than to a consistent response across all members of the group. Thus, we used a within-subjects design, common in primate studies, with each condition tested in counterbalanced order on each subject. In this way, we got a measure of the number of individuals who showed behavior consistent with an endowment effect. In order to better compare our results to those from human studies, we also analyzed the change in the groups' mean behavior between each condition.

Thus, the current study specifically addressed the role of how an object's immediate usefulness affected the endowment effect by using exchange items, tools, which varied in whether they could be immediately used to obtain food, but were otherwise identical between conditions. We hypothesized that the tool's situational value would influence the endowment effect. Specifically, we predicted a stronger endowment effect when tools were useful (i.e., when both foods were available) than when the tools were not useful (either because the food was absent, or it was present but not available). Secondarily, we utilized both individual- and group-level analyses to best understand the variation within chimpanzees, as well as how these results compared to those of humans.

2. Methods

2.1. Participants

Participants were 20 adult chimpanzees (10 male, 10 female) housed at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center. Chimpanzees were housed in social groups in large outdoor enclosures with climbing structures, toys, and additional enrichment. Each outdoor compound also included an indoor area of dens, where all testing took place. Subjects received biscuits and water ad libitum and four daily enrichment meals.

Subjects were already proficient at exchanging objects with a human for a food reward. This was essential for the task, as subjects who were disinclined to exchange would artificially inflate the results indicative of an endowment effect. Thus, prior to commencing the study, we verified that each subject would exchange with the human experimenter. All subjects completed a session of exchange with the experimenter in which they were required to return an object 10 times in a row. All subjects passed this pretest.

Because the experiment involved tools, it was also important to verify that each chimpanzee could use each tool equally proficiently. To ensure subjects understood the task and tools, we chose two ecologically relevant tasks they experienced routinely as part of their regular enrichment. The first task was a dipping task in which subjects could use a stick to obtain oatmeal (similar to a honey dipping task), and the second was a sponging task in which subjects could use paper wads to obtain juice (details of both are below). All subjects received a series of sessions in which they were given both of the tasks individually, with the appropriate tool, to verify that they could use the tool to obtain the appropriate food.

2.2. Tools

Items for exchange consisted of two tools: a sponge that could be used to obtain juice (50% grape juice, 50% water) and a dipstick that could be used to obtain oatmeal (instant maple brown sugar flavor). These foods were chosen because pilot testing using chimpanzees that were not a part of the study (to avoid differential exposure to the objects prior to testing) showed similar preferences for the two. The sponge consisted of an approximately 30×40-cm piece of absorbent butcher paper that chimpanzees wadded and dipped into juice available in a trough outside of their enclosure. The dipstick was a cardboard lollipop stick approximately 29 cm in length that could be dipped in the hole of the oatmeal container to obtain oatmeal. The oatmeal container was also located outside of the subjects' enclosure, and its hole was too small to admit fingers or any tool other than the provided stick. Neither food could be obtained without the appropriate tool or with the alternate tool.

2.3. Procedure

Tests were divided into three Treatments of three tests each. In the first Treatment (the Absent Treatment), no food was present during any of the four tests. In the second Treatment (the Unobtainable Treatment), both foods were visible and present, but beyond the chimpanzees' reach during all four tests. Thus, subjects could clearly see the foods, but were unable to use the tools to access them. After the completion of the subjects' session, foods were removed without the chimpanzees having access to them, so they had no expectation that rewards would be available at a later time. In the third Treatment (the Obtainable Treatment), both foods were present and obtainable with the corresponding tool during all tests. Note that in the Unobtainable and Obtainable Treatments, both foods were always present simultaneously and for the duration of the test; the difference lay in whether the foods could be accessed. The Absent Treatment control was run twice, prior to each of the other two Treatments, to verify that the subjects' behavior toward the tools did not change with the experience provided in the first Treatment in which food was present.

Each Treatment consisted of a Preference Condition and two Endowment Conditions. In the Preference Condition, subjects were given a simultaneous choice between the two tools and indicated their preference by reaching for their preferred item. Tools were presented on a predetermined side, which was counterbalanced across chimpanzees. The experimenter held both objects out, approximately 20 cm apart and at eye level to the chimpanzee, and called the chimpanzee's attention to them. Once the chimpanzee was watching, the experimenter moved both objects forward to within 5 cm of the caging. Subjects could indicate their preference by reaching with their hand or their pursed lips (some subjects had previously been trained to accept foods with their lips and so were allowed to indicate preference however they preferred). Whichever object they reached for was then given to them (Brosnan & de Waal, 2004).

In the Endowment Conditions, subjects were given a predetermined tool and then given the option to keep it or exchange it for another. The experimenter again held both tools out, at the chimpanzee's eye level, approximately 20 cm away and called the chimpanzee's attention to them. Once the chimpanzee was watching, the experimenter handed the predetermined tool to the chimpanzee. The experimenter then offered an exchange immediately (as is typical in human endowment effect experiments) with the second tool in her right hand (it was moved to the right hand if it was not already there; object presentation was counterbalanced) and moved it forward to within 5 cm of the caging. At the same time, the experimenter held her left hand out, palm up, at the chimpanzee's chest level, the cue that is always used to offer an exchange. The experimenter did not use any words or cues (e.g., a clicker) that might have indicated that the chimpanzee was expected to exchange. Subjects had the opportunity to exchange until they used the tool or 30 s elapsed, whichever came first (Brosnan et al., 2007). In practice, the subject always either exchanged or used the tool within a few seconds. Thus, for the Dipstick Endowment Condition, subjects were endowed with the dipstick and could exchange for the sponge; in the Sponge Endowment Condition, subjects were endowed with the sponge and could exchange for the dipstick. Again, whenever foods were present (e.g., the Obtainable and Unobtainable Treatments), both foods were available simultaneously in all three of the Conditions, so subjects had access to both—or neither—simultaneously.

Treatments were presented in a set order, but the three conditions were randomized for each subject within each Treatment. Subjects first completed the Absent Treatment (as an initial control) followed by the Obtainable Treatment. To verify that obtaining a food did not change their preferences, subjects were given a second Absent Treatment followed by the Unobtainable Treatment; results did not differ between the Absent Treatments (Wilcoxon signed ranks tests: preference: $T+=6$, $n=10$, $p=.527$; endowed sponge: $T+=1$, $n=3$, $p=.564$; endowed dipstick: $T+=0$, $n=1$, $p=.317$), so these Treatments were combined for most analyses (exceptions are indicated).

Each of the 20 subjects completed a series of 12 tests, with each test completed on a different day. Thus, subjects had only a single choice a day. In order to minimize possible effects of habituation, subjects typically received two to three choices per week. Subjects were tested between 10:30 and 15:30, and no testing occurred prior to the first enrichment feeding of the day (primate chow and water were available ad libitum). In this way, all subjects had had access to preferred foods prior to their day's choice, regardless of when they were tested. Tests consisted of one session each of the Available and Unobtainable Treatments, each of which consisted of three Conditions, and two of the Absent Treatments, also consisting of three Conditions, with one Absent Treatment before each of the other two Treatments.

2.4. Individual-level vs. group-level analyses

This methodology was based on a human design. However, one weakness of the human literature on the endowment effect is that results are virtually always compared across groups (i.e., a between-subjects design), rather than within individuals (i.e., a within-subjects design). For example, while humans are known to maintain possession of objects at higher levels than expected due to their preferences, those preferences were obtained from a different group of individuals. Group-level analysis obscures variation and does not allow analysis of individual trends.

Previous research on 32 chimpanzees indicated that while the group-level effect (i.e., the group-level change in preference, the typical level of analysis for human studies) was similar to that seen in humans, there was quite a lot of variation in individuals' behavior (Brosnan et al., 2007). Thus, we analyzed the current data in two ways. First, we assessed how many chimpanzees actually showed an endowment effect. For this, we assessed whether each individual showed behavior consistent with an endowment effect, retaining possession of tools despite his or her separately expressed preference, and then analyzed whether the distribution of individuals with each of the four possible outcomes (see below) differed from chance. To do this, each chimpanzee was given a score of 1 (exchanged neither tool; the only outcome strongly indicative of an endowment effect), 2 (exchanged both tools; indicative of a preference for interaction), 3 (exchanged the preferred tool, while keeping the nonpreferred tool; behavior inconsistent with preferences), or 4 (exchanged the nonpreferred tool, while keeping the preferred tool; behavior consistent with preferences). Although there could in theory be some behavior reflecting an endowment effect hidden within conditions 3 and 4, the most rigorous test, which we employed, is to consider as evidence of an endowment effect only those cases in which individuals refused to exchange *both* tools. This avoids the possibility of considering individuals who were potentially disinterested in the task (outcome 3) or were simply following their preferences, with no influence of possession on the strength of those preferences (outcome). We then did a Friedman's test to see if there was variation across the group in their behavior. Considering the data in this way allowed us to more fully quantify what happens at the individual level. Second, we assessed the percent change in preference between Conditions due to the Treatments across the entire group of chimpanzees tested. That is, considering the mean responses, were chimpanzees, on average, more likely to exchange than would be anticipated based on the mean preference results? While we believe that this latter approach is less informative, it did allow us to compare these results to those of humans.

2.5. Analysis

Since the sample size of chimpanzees was only 20, we used nonparametric statistics for all analyses. Comparisons across multiple dimensions were done using Friedman's tests, which take into account repeated measures, and paired comparisons were done using the Wilcoxon signed ranks test. In Wilcoxon tests, the reported sample sizes (ns) differed from 20 due to ties, which are not considered in the calculation of the final statistic. Significance was considered to be $p<.05$. All statistical tests were two-tailed.

3. Results

3.1. Effect of Treatments and Conditions on chimpanzees' exchange behavior

There was a strong effect of Treatment on behavior, with subjects behaving differently in the Obtainable than in the other two Treatments. Specifically, despite the data from our initial preference tests with chimpanzees not used in the study (to avoid contamination) that indicated similar preferences for the two tools, the experimental subjects preferred the sponge over the dipstick in all conditions. Nonetheless, the preference was significantly stronger in the Obtainable Treatment as compared to the other two Treatments (preference for sponge; Absent: 70%, Unobtainable: 70%, Obtainable: 100%; χ^2_2=7.74, p=.025).

Considering the Endowment Conditions, in both the dipstick-endowed and sponge-endowed Conditions, subjects exchanged significantly less often in the Obtainable Treatment than in the Absent and Unobtainable Treatments indicating a stronger preference to keep whichever tool they had been given when food was currently available (frequency with which subjects exchanged the dipstick for the sponge; Absent: 97.5%, Unobtainable: 100%, Obtainable: 55%; Friedman's test: χ^2_2=25.83, p<.001; frequency with which the subjects exchanged the sponge for the dipstick; Absent: 72.5%, Unobtainable: 80%, Obtainable: 15%; χ^2_2=22.81, p<.001). In other words, subjects were significantly more likely to exchange the tool for another when food was not currently accessible. However, if food was available (i.e., the Obtainable Treatment), chimpanzees instead preferred to keep whichever tool they received, regardless of whether it was the sponge or the dipstick.

3.2. How many chimpanzees show the endowment effect?

We first examined how individuals behaved. Despite the prevalence of group-based measures in the human literature (see below for group-based measures in this study to allow for comparison with humans' results), we felt that an individual approach was more appropriate approach as it uncovered variation hidden in a group-level analysis as well as opening future possibilities to study how other factors may interact with the response at the individual (rather than group) level. In our study, each individual could display one of four behaviors: (1) exchanged neither tool, (2) exchanged both tools, (3) exchanged only the preferred tool, or (4) exchanged only the nonpreferred tool. The first behavior is the only one that indicated an endowment effect.

Individuals' exchange behavior varied significantly across the different Treatments. In the Absent and Unobtainable Treatments, in which food was not available, more than 70% of individuals exchanged both tools, a significantly greater percentage than for any of the other three possibilities (Absent 1: χ^2_2=9.70, p=.008; Absent 2: χ^2_2=15.7, p<.001; Unobtainable: χ^2_2=19.90, p<.001, Fig. 1). No individual kept both tools (the behavioral option most consistent with an

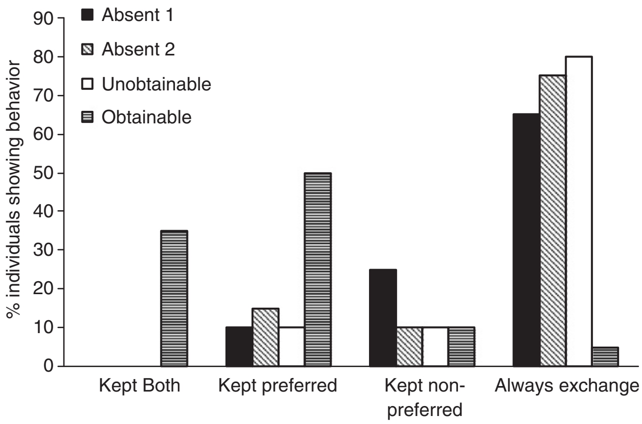

Fig. 1. Individually, subjects were least likely to keep a tool in the Absent and Unobtainable Treatments, and never showed an endowment effect (i.e., never kept both items). However, in the Obtainable Treatment, subjects typically either kept both tools (revealing an endowment effect) or kept their preferred tool. *X*-axis labels indicate whether subjects kept or exchanged the tools.

endowment effect) in either of these Treatments. In contrast, in the Obtainable Treatment, a third of subjects (33%) showed behavior consistent with an endowment effect, keeping both objects. Moreover, while only approximately 10% of subjects even kept their preferred tool in the Absent and Unobtainable Treatments, half of subjects (50%) did so in the Obtainable Treatment (the sponge was preferred for all subjects; χ^2_2=10.80, p=.013), which could potentially indicate a stronger endowment effect in the latter context. Finally, in contrast to the previous two Treatments, in which 70% of subjects exchanged both items, fewer than 5% of subjects did so in the Obtainable Treatment.

Thus, when the tools are immediately useful, we found evidence for an endowment effect in approximately one third of our subjects, as compared to none in either of the two Treatments in which food was not immediately available. In comparison, in previous work, we found that 42% of chimpanzees showed evidence of an endowment effect for foods, while <5% (one subject) did so for nonuseful nonfoods (in that case, toys that could not be used to obtain food; Brosnan et al., 2007). Thus, these results were very consistent when comparing conditions both within studies as well as across studies. Moreover, we found additional evidence that subjects were sensitive to the presence or absence of food; in the Obtainable Treatment, most of the rest of the subjects showed the exchange behavior that is expected based on their preferences, while the vast majority exchanged in all circumstances in the other two Treatments.

3.3. Group-level presence of the endowment effect

There are remarkably few human studies of the endowment effect that have reported individual data (the most definitive meta-analysis of endowment effect studies, Sayman & Oncluler, 2005, identified only two human studies that reported results from within-subject designs; this reflects the concern that, in humans, any past experience with a given exchangeable good could confound a person's future valuation of that good). Thus, while we considered this group-level analysis less informative than the previous, individual results, we here report the results of a group-level analysis based on the subjects' mean responses in order to compare these results to those of humans. For this analysis, we compared whether the subjects' mean responses differed across the three Treatments, as is typically done in human studies. To do so, we compared the group-level tendency to keep objects initially given in the Endowment Conditions to the group-level preferences expressed in the Preference Condition. Again, subjects as a group behaved very differently in the Obtainable Treatment than in the other two Treatments, in which food was not obtainable. Comparing the difference between the Preference and Endowment Conditions across all three Treatments, we found that subjects were much more likely to keep each of the tools in the Obtainable Treatment than in the Absent and Unobtainable Treatments (Friedman's test, sponge: χ^2_2=19.6, p<.001; dipstick: χ^2_2=16.222, p<.001).

Specifically, in the Absent Treatments, subjects were significantly less likely than predicted to keep either tool, based on the group-level behavior in the preference tests. Twice as many subjects exchanged the sponge in the Endowment Condition as expected based on the preference test results (Fig. 2: 70% vs. 27.5%; Wilcoxon signed rank test Absent 1: T+=3, N=13, p=.052; Absent 2: T+=0, N=10, p=.002), and 12 times as many exchanged the dipstick as expected (30% vs. 2.5%; Absent 1: T+=1, N=14, p=.001; Absent 2: T+=0, N=15, p<.001). Despite the fact that food was present, if unreachable, in the Unobtainable Treatment, three times as many subjects exchanged the

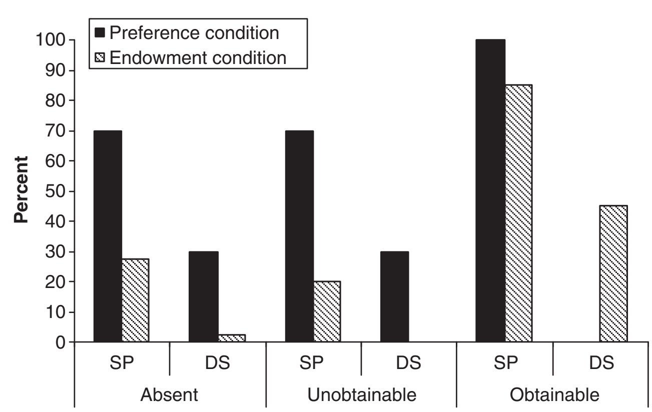

Fig. 2. The percent of subjects who chose to keep the endowed tool (e.g., rather than exchange for the other tool; Endowment Condition) versus the percent of subjects who chose the tool in a choice task (Preference Condition). When given the opportunity to exchange, subjects were less likely to keep a given tool (hatched bars) in the Absent and Unobtainable Treatments than indicated by their preference (solid bars). They were equally or more likely to keep a tool in the Obtainable Treatment (Absent Treatments are combined). SP: sponge; DS: dipstick. The *Y*-axis indicates the percent of subjects who chose the tool in the Preference Condition and the percent of subjects who retained the tool in the Endowment Condition.

sponge in the Endowment Condition as expected based on the Preference Condition (70% vs. 20%; $T+=12$, $N=14$, $p=.008$), and all subjects exchanged the dipstick, despite preferring it to the sponge only 30% of the time in the Preference Condition (30% vs. 0%; $T+=0$, $N=14$, $p<.001$). Thus, in these two conditions, in which food could not be accessed, subjects were actually more likely to exchange than their preferences indicate.

In sharp contrast, in the Obtainable Treatment, subjects showed a reduced tendency to exchange either object. As opposed to the other two Treatments, chimpanzees kept the dipstick 45% of the time (i.e., exchanged it 55% of the time), despite never choosing it when given the choice (Preference Condition: 45% vs. 0%; $T+=0$, $N=11$, $p=.001$) and exchanging it every single time in the Unobtainable Treatment. These results indicate a strong endowment effect. Unfortunately, despite our efforts to choose tools of equal value based on pilot testing of nonsubject chimpanzees, subjects used in the experiment showed a strong preference for the sponge. While this does not preclude an endowment effect, it did lead to a ceiling effect; although subjects kept the sponge on every single trial in the Obtainable Treatment, the mean was not significantly higher than in the Preference Condition (100% vs. 85%; $T+=0$, $N=3$, $p=.083$). Nonetheless, the trend was in the direction of an endowment effect.

4. Discussion

We found that the endowment effect varies markedly as a function of an object's immediate usefulness, a phenomenon that has not been previously demonstrated and may serve to explain some of the variability in the strength of the effect in both humans and other species. This bias in chimpanzees changed dramatically depending on whether tools that otherwise lacked inherent value could be used at the time of possession to obtain food. Specifically, when foods were either not present at all or present but unobtainable, subjects manifested no endowment effect for the tools. However, as predicted, when food was present and available, chimpanzees showed robust endowment effects for the very same tools; that is, they refused to exchange both tools, their less preferred as well as their more preferred. Importantly, this bias varied not as a function of the mere presence of the food, but rather it was entirely contingent on the current possibility of using the tools to obtain food. These findings support the hypothesis that the endowment effect is the result of evolutionary pressures to maximize outcomes during inherently risky exchange interactions. In situations in which there was much to lose, exchange may have been too risky, leading to a tendency to hold on to a less preferred object even when a more preferred one is offered in exchange.

Thus, our data indicate that the variation seen in the endowment effect is predictable based on at least one factor: whether the object is useful in the current context. The fact that this variation is consistent and can be predicted based on features external to the experimental procedure supports the conclusion that this situational dependence evolved to maximize outcomes in different situations (Todd & Gigerenzer, 2007) and that the context of the interaction—in this case, the object's usefulness—is at least as important as the actual act of possession. Thus, when considering the endowment effect, a specific bias, it may often be just as important to attend to the situation as it is to attend to the mere state of possession. That is, endowment may be a piece of the puzzle, but an endowment in a context lacking immediate usefulness may not evoke the bias.

These data extend previous findings indicating that endowment effects in great apes can differ as a function of the object at issue, as is true in humans (Brosnan et al., 2007; Flemming et al., in review). Given the potential to trade food items in a similar design to this study, both chimpanzees and orangutans showed an endowment effect of roughly equivalent magnitude to that seen in some human studies. As predicted, this was not true for toys. However, those studies confounded salience with other possibilities, such as categorical differences in interest in the two types of items. The present study disentangles these possibilities and, more importantly, shows that the endowment effect can actually shift for the same item dependent upon whether the item is useful in a given situation. Thus, the present results cannot be explained by differences in preference between types of items, but can be explained by changes in item usefulness as situations change.

As with previous data on chimpanzees, our data also indicate that this effect can be the result of only a subset of the group displaying the behavior. There are several possibilities for this individual variation. First, endowment effects are likely to vary in strength between individuals, based on either (or both) innate predispositions or previous experience. Second, while we have relative preference data between these two tools for all individuals, it may be that some individuals had stronger or weaker preferences than others, or that they got differential enjoyment out of the task. Of course, the most critical point is that these effects appear across multiple species, including humans (Brosnan et al., 2007; Flemming et al., in review; Lakshminarayanan et al., 2008). Thus, while it may be that the effect does not appear in all individuals or in all situations, this does not contraindicate a selective benefit for the bias. The fact that a behavior has evolved due to selective pressure does not mean that it must manifest at every opportunity, nor does the fact that a behavior occasionally may not be beneficial make it any less likely to evolve. Nonetheless, one very important implication of these findings is the need for additional research on individual-level endowment effects among humans.

Virtually all studies report group-based differences from between-subjects designs, precluding any investigation of individuals' behavior. However, our results indicate that endowment effects on the magnitude of those seen in humans can be the result of only some individuals' behavior. Future research in humans is needed to determine the relative contribution of individuals. Such studies will also help to clarify how individual factors such as experience, culture, personality, etc., affect cognitive biases, necessary steps to effectively address them. For instance, given that the endowment effect is hypothesized to have evolved in the context of risky trade situations, an obvious hypothesis is that the strength of the endowment effect in an individual should correlate with the individual's relative risk sensitivity, with more risk-sensitive individuals displaying the endowment effect in more situations. Hypotheses such as these cannot be tested with the current group-level approach that is common amongst human studies.

These data, in concert with those from the previous studies, indicate that suites of cognitive and behavioral biases in humans cannot be adequately explained by inevitable constraints on decision-making (such as limitations on cognitive processing power, processing time, etc.; Conlisk, 1996) or by any psychological phenomenon limited to humans themselves. Humans are not the only species to show biases, indicating that these behaviors likely evolved prior to the human split from other species. This has two implications. First, it is clear that we can learn about the development and function of biases from studying their prevalence and distribution in other species. Such a comparative approach provides a broader background, as well as an opportunity to investigate these behaviors removed from modern human culture.

Second, the widespread presence of endowment effects as well as other behaviors (e.g., loss aversion), indicates that these are not quirks that require justification, but instead are robust features that evolved in primates (at a minimum—even amoebas show "irrational" behavior in some contexts; Latty & Beekman, 2010). Such prevalence is unlikely if these behaviors were not specifically selected due to their beneficial results. In other species, it is likely very risky to trade an object away because, without a skill such as language, it is difficult or impossible to police interactions and to eliminate cheaters (Brosnan, in press; Brosnan & Beran, 2009; Brosnan, Grady, Lambeth, Schapiro, & Beran, 2008). Humans have used language to develop extensive control mechanisms (e.g., the system of law enforcement, the court system) that provide an unprecedented opportunity for an individual to interact with others with less fear of his or her partner cheating. Thus, while the endowment effect seems illogical and even detrimental in modern Western societies, it was likely essential to earlier humans, as well as other species. This is not to say that this does not require further investigation. From the broader perspective, understanding the contexts likely to elicit the endowment effect is important for two reasons.

First, in humans, this bias has far-reaching legal and social implications because vast personal and market transactions involve exchanges in, and sales of, goods and rights. Regulators may assume that goods and rights will ultimately end up in the hands of those who value them the most (at least when transaction costs are minimal; Coase, 1960), making end distributions relatively insensitive to initial distributions. But endowment effects can make goods and rights "sticky"—that is, likely to stay in the hands of those into whose hands they happen to first get. In such cases, endowment effects can undermine efficient markets and allocations in goods and rights (Jolls, Sunstein, & Thaler, 1998; Korobkin, 2003). Second, as argued earlier (Gigerenzer et al., 1999; Haselton et al., 2009; Jones, 2001; Jones & Brosnan, 2008; Jones & Goldsmith, 2005), the ability to use an evolutionary perspective to predict novel, specific, context-dependent variation in one bias suggests that the same may be true for others as well. A better appreciation for the evolution of these behavioral predispositions may illuminate their function (i.e., the reason natural selection favored them), which in turn will help with predictions of the situations and contexts in which various biases can—or cannot—be expected to emerge.

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