

The Evolutionary Origins of Human Patience: Temporal Preferences in Chimpanzees, Bonobos, and Human Adults

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Summary

To make adaptive choices, individuals must sometimes exhibit patience, forgoing immediate benefits to acquire more valuable future rewards [1–3]. Although humans account for future consequences when making temporal decisions [4], many animal species wait only a few seconds for delayed benefits [5–10]. Current research thus suggests a phylogenetic gap between patient humans and impulsive, present-oriented animals [9, 11], a distinction with implications for our understanding of economic decision making [12] and the origins of human cooperation [13]. On the basis of a series of experimental results, we reject this conclusion. First, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) exhibit a degree of patience not seen in other animals tested thus far. Second, humans are less willing to wait for food rewards than are chimpanzees. Third, humans are more willing to wait for monetary rewards than for food, and show the highest degree of patience only in response to decisions about money involving low opportunity costs. These findings suggest that core components of the capacity for future-oriented decisions evolved before the human lineage diverged from apes. Moreover, the different levels of patience that humans exhibit might be driven by fundamental differences in the mechanisms representing biological versus abstract rewards.

Results

When asked to decide between ten dollars in 30 days and 11 dollars in 31 days, people typically prefer the larger reward. However, when asked to choose between ten dollars now and 11 dollars tomorrow, people are more impulsive and prefer the immediate reward [3, 4]. These inconsistent preferences reveal that people often

trade off between immediate and future benefits. Non-human animals must also make time-sensitive decisions about mating or foraging in their natural environments [1, 14]. Experiments with captive birds, rodents, and primates [5–10], however, show that many nonhuman species wait less than a minute (often only a few seconds) for a larger, delayed food reward when offered an immediate alternative. Relative to humans, who will frequently wait weeks or months for larger monetary rewards [4], animals thus appear to be impulsive over a radically reduced timescale.

These extreme differences between humans and nonhumans seem to provide powerful evidence that patience is a uniquely human trait (as suggested by [11, 12, 15]). But is this cognitive divide real? Some chimpanzees can wait several minutes in delay of gratification and exchange tasks [16–18], suggesting higher levels of patience in other hominoids. Two pieces of evidence are therefore required to test the uniqueness of human patience. First, if our species' temporal preferences originated in the human lineage, then our two closest phylogenetic relatives—bonobos and chimpanzees—should make impulsive decisions like other animals. Second, humans should wait longer than animals in directly comparable contexts—such as during decisions about food, a currency with more direct evolutionary relevance.

We provide a systematic test of these predictions by (1) comparing the temporal preferences of bonobos, chimpanzees, and humans in a food task, and (2) examining human temporal preferences across contexts—for iterated choices involving food or money, and in response to more typical discounting questionnaires. Our iterated task differed from standard economic tasks in several ways. First, subjects select between real rather than hypothetical (e.g., [19]) or partially realized (e.g., [20]) rewards. Second, subjects experience delays and pay an opportunity cost for waiting because they cannot concurrently engage in other activities or proceed to the next decision. Increasing evidence suggests that both the experience of delays [15, 21, 22] and variations in reward type [19, 23–26] can influence human preferences. Nonetheless, the majority of studies investigating human temporal choice involve low-cost choices about money, an evolutionarily novel reward that only humans are motivated to acquire [27]. In contrast, most animal studies necessarily involve biological rewards and higher opportunity costs. Thus, by letting human subjects make decisions about food rewards and experience delays, we offer a more appropriate methodology for comparison across species.

Study 1: Temporal Preferences in Bonobos and Chimpanzees

In the first study, we characterized the temporal preferences of chimpanzees and bonobos, determining the delay at which they chose equally between a smaller, immediate food reward, and larger, delayed food reward

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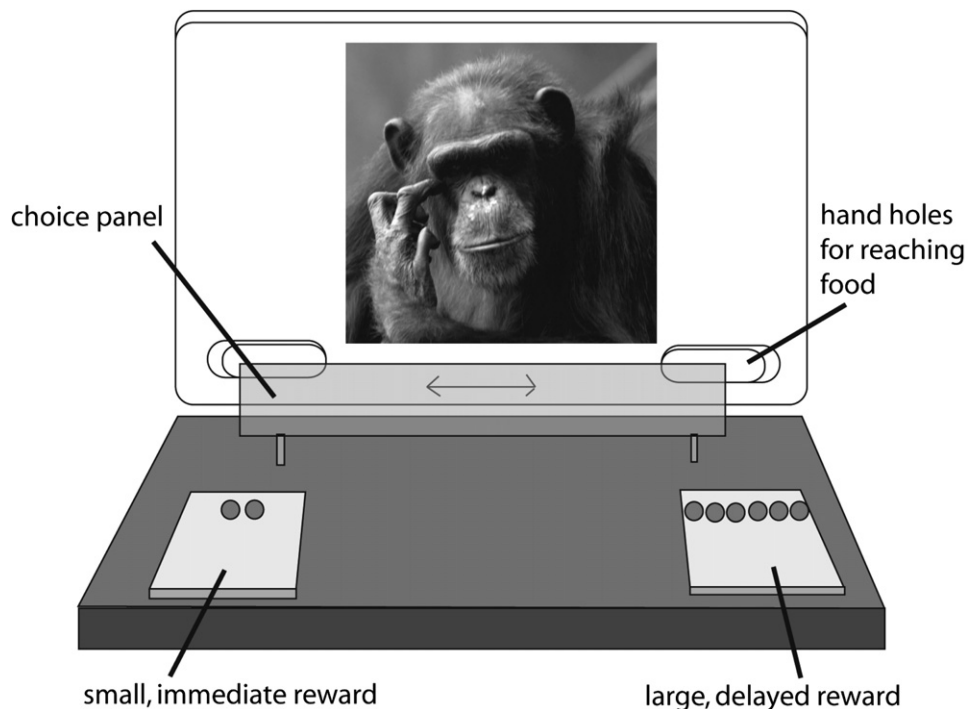


Figure 1. The Ape Discounting Apparatus Used in Studies 1 and 2

Subjects could choose between a small, immediate reward (two grape halves) and a large, delayed reward (six grape halves). Subjects faced the experimenter (E) through a Plexiglas panel; this panel had hand holes on either side so subjects could insert their fingers to make choices. E sat in front of a Table (75 × 40 × 50 cm) with two sliding platforms (9 × 12 cm) for food rewards (side assignment was counterbalanced within a session). Each trial started when E removed an occluder blocking access to the table; subjects then had 15 s to indicate a choice. Subjects indicated their preference by sliding the choice panel (70 cm wide, 9 cm tall, attached to the front of the table) to uncover either the left or right hole, and then could access their chosen food option when E slid the platform forward (immediately if subjects chose an immediate reward, but after a delay if they chose a delayed reward). E removed the forgone option after the subject made a choice. Subjects could take as long as they wanted to eat the food, and a trial ended when the subject placed the last piece of food in her mouth. E then replaced the occluder; the next trial began after a 30 s intertrial interval (ITI). Subjects in both studies completed no more than one session per day.

(as in [6, 8]; Figure 1). Bonobos showed indifference when the larger reward was delayed by a mean of 74.4 s (standard error [SE] = ± 8.5 s), whereas chimpanzees waited a mean of 122.6 s (SE = ± 15.9 s), a significantly longer period [$t(8) = 2.68$, $p = 0.03$, two tailed]. Both species waited longer than did other animals previously tested in a similar manner [6, 8], including other primates (Figure 2). Finally, neither species' pattern of data can be explained by the short-term maximization of intake rate over repeated trials, a model that has been successfully applied to the choices of other non-humans [5, 8]. This suggests that the apes made decisions over longer temporal horizons than did other animals. Accordingly, a long-term rate-maximizing currency [28], which is more farsighted than most species' patterns of choice (see [14] for a review), can account for the bonobos' preferences. However, chimpanzees are significantly more patient than expected by this model (see the Supplemental Data available online). That is, chimpanzees and bonobos exhibit different temporal preferences than do other nonhumans examined thus far, and available models of choice cannot entirely account for this difference.

Study 2: Comparison of Patience in Humans and Chimpanzees

Although both ape species waited longer than other animals for food rewards, humans express a willingness

to wait days or even years to acquire monetary rewards [4]. Consequently, here we provide the first direct comparison of chimpanzee ($n = 19$) and human ($n = 40$) temporal preferences; bonobos could not be included because of sample size limits. The two species made a series of choices between a smaller food reward (two pieces) and larger reward (six pieces): In the delay condition, the small reward was available immediately and the large reward was available only after a 2 min delay, whereas in the control condition, both options were available immediately. The control condition therefore measured subjects' baseline motivation to choose the larger reward, and assessed possible changes in motivation due to food consumption. Each human participant experienced one condition, whereas chimpanzees experienced both in a counterbalanced order.

We first compared the preferences of the human participants ($n = 20$ per condition) and the chimpanzees in their first test session (to ensure that prior experience did not influence chimpanzees; delay condition $n = 10$, control condition $n = 9$). Figure 3 shows that although both species strongly preferred the larger reward when available immediately (percent choice: chimpanzees = $88.9 \pm 4.8\%$, humans = $77.5 \pm 7.4\%$), only chimpanzees maintained this preference when required to wait two minutes (chimpanzees = $71.7 \pm 6.6\%$, humans = $19.2 \pm 4.4\%$; Figure 3). Condition [repeated-measures analysis of variance (ANOVA): $F(1, 55) = 29.16$, $p < 0.001$] and

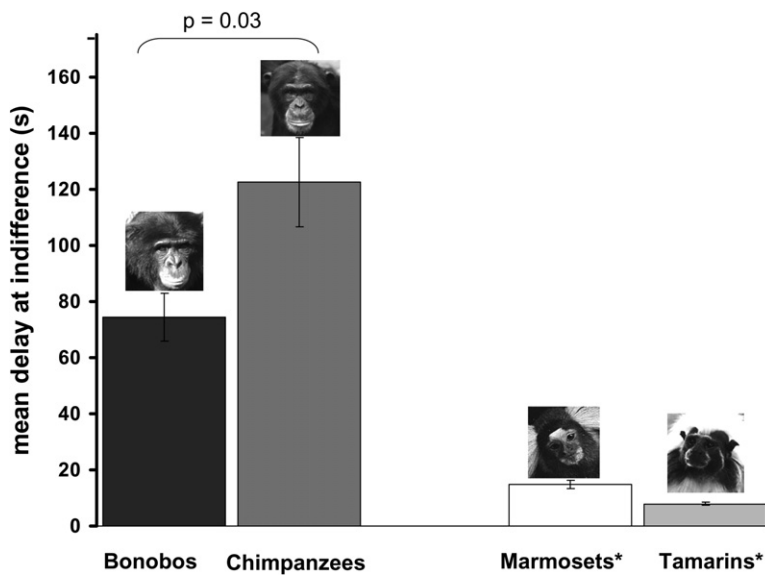


Figure 2. Delay at Indifference for Various Primate Species

In study 1, bonobos and chimpanzees chose between two pieces of food available immediately and six pieces of food available after some delay. Stevens et al. 2005 [8] found indifference points in a similar manner for common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*). Error bars represent standard error of the mean indifference point for each species.

species [$F(1, 55) = 18.78, p < 0.001$] influenced choices, but not session half [$F(1, 55) = 0.36, p = 0.55$]. An interaction between species and condition [$F(1, 55) = 8.73, p < 0.005$] showed that although the species did not differ in the control condition, humans chose the larger reward significantly less often in the delay condition than in the control condition, and less than chimpanzees overall (Tukey post-hoc tests; $p < 0.005$ for all significant cases).

To confirm that chimpanzees were sensitive to the delay, we next used a within-subjects analysis comparing individual chimpanzees' choices across both conditions. Overall, chimpanzees chose the large reward more in the control condition [control condition = $89.5 \pm 3.2\%$, delay condition = $66.7 \pm 4.8\%$; paired $t(18) = 4.10, p < 0.001$ two tailed]. Both species therefore made trade-offs between rewards and time, although chimpanzees exhibited greater patience than did humans when required to wait for the larger payoff (Movies S1 and S2).

Humans might not have waited in the delay condition because they did not wish to consume larger quantities of food. Three lines of evidence suggest this is not the case. First, both species strongly preferred the larger reward in the control condition—and whereas the chimpanzees' preference for the larger reward dropped by 19% in the delay condition, the human subjects' preference dropped by 75%. Second, neither species' preferences changed across sessions in either condition, indicating that the humans did not stop choosing the larger amount because they become satiated over repeated trials. Finally, an additional analysis indicates that their choices in the delay condition were not due to a lack of hunger (see the Supplemental Data).

Comparative analyses of cognition are notoriously difficult to conduct because of the inherent difficulty of equating methodologies across species. In the present study, chimpanzees and humans might not have faced identical waiting costs nor had an identical desire for the food. That said, neither species was food deprived, both could access food outside the test, and neither showed evidence of satiation. Altogether, these results suggest that humans and apes show comparable preferences when confronted with very similar temporal decisions.

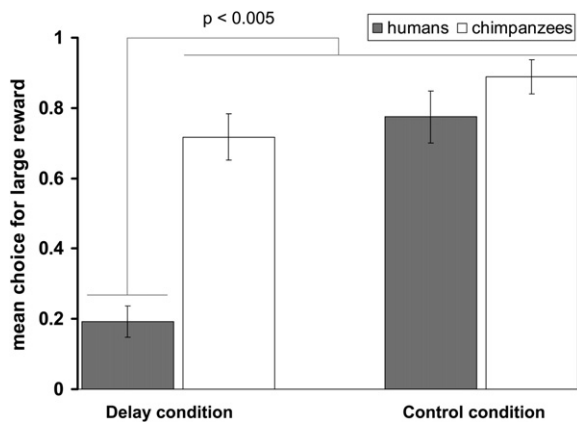


Figure 3. Human and Chimpanzee Preferences for Larger Food Rewards

In the delay condition (study 2), subjects chose between two food items available immediately and six food items available after 2 min, whereas in the control condition, both reward amounts were available immediately. Chimpanzee data is from their first test session. Error bars represent standard error of mean proportional choice for the larger reward.

Study 3: Human Patience and Reward Type

In study 2, human participants showed markedly different behavior in response to the iterated food problems than they do in more typical decisions involving money. We therefore conducted a third study to assess how reward type (money or food) and experiential context (real or hypothetical money and delays) impacts human decision making. A new group of human participants ($n = 20$) made iterated temporal decisions like those in study 2, but over small amounts of money (20 cents now versus 60 cents after 2 min). On average, participants waited on 56.7% of trials [$SE = \pm 8.8\%$]. Comparing these participants to those from the delayed food condition showed that people were more than three times as willing to wait for small amounts of money than for food [$t(38) = 3.839, p = 0.001$, two tailed]

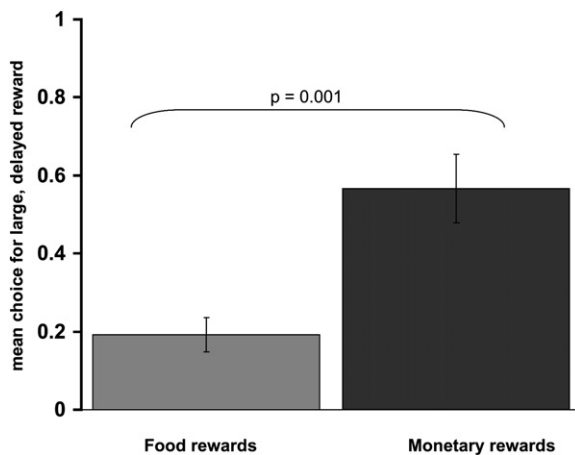


Figure 4. Human Preference for Delayed Food and Money

Subjects chose between a larger, delayed reward and a smaller, immediate alternative during an iterated, experiential discounting task involving either food rewards (delay condition, study 2) or monetary rewards (study 3). Error bars represent standard error of mean proportional choice for the delayed reward.

(Figure 4). Individual subject data shows that whereas 40% of subjects in the delayed money condition waited every trial to receive an additional 40 cents, not a single subject did so to acquire more food. Critically, this result rules out the possibility that subjects in the delayed food condition did not wait because the paradigm was inherently aversive: Subjects in the delayed money condition faced an identical situation and opportunity costs, but were frequently willing to wait for more rewards.

As a final test, we examined all human participants' ($n = 60$) preferences on a hypothetical discounting questionnaire; such questionnaires carry low opportunity costs for choosing the larger reward. We used participants' responses over a series of ten questions (e.g., "Would you prefer to receive \$31 today or \$59 in 150 days?") to calculate the hyperbolic discounting factor (k), frequently used as an index of discounting levels in such contexts. Consistent with past findings, subjects exhibited a mean discount factor of $k = 0.0116$ (see the Supplemental Data). This value predicts that participants would be willing to wait up to 172 days for 60 dollars over an immediate 20 dollars—in contrast to their more impulsive preferences when required to actually wait 2 min delays to acquire food or money.

Discussion

Our results demonstrate that humans share similar levels of patience with bonobos and chimpanzees in some contexts. Both members of the *Pan* genus preferred to wait for larger delayed rewards, and did so for longer periods than other nonhuman animals tested thus far. Additionally, chimpanzees were actually more patient than humans when compared on similar temporal tasks. We conclude that a capacity for patience in the context of food rewards evolved before the human lineage split. Based on the comparative evidence, we also suggest that the last common ancestor of *Homo* and *Pan* possessed an extended temporal horizon for

decisions about food. Because short temporal horizons could preclude the evolution of sophisticated capacities such as mental time travel [11] or reciprocal altruism [13], these findings imply that apes' abilities to plan for future activities [29, 30] or engage in flexible cooperative interactions [31, 32] might have arisen once the constraint of impulsivity was lifted.

Higher tolerance for delayed food rewards could have evolved as a foraging adaptation, and variation between closely related species might reflect differences in their natural ecology. For example, the varying levels of patience exhibited by callitrichid monkeys across contexts maps onto differences in their wild foraging patterns [8, 33]. Notably, chimpanzees inhabit environments characterized by small, unpredictable food patches with unstable fruit availability, whereas bonobos live in comparatively productive environments [34, 35]. Accordingly, variation in habitat has been proposed as a major selective force shaping the disparate social behaviors of *Pan* [36]. We suggest that ecology might also underlie differences in *Pan*'s nonsocial cognition: Chimpanzees may generally tolerate higher additional costs to procure food, such as increased work effort, longer travel distances, and the temporal costs explored here. Notably, there is extensive evidence for hunting and extractive tool technology in wild chimpanzees but not bonobos. Their respective temporal preferences might therefore promote optimal foraging rates in their different natural ecologies, although not necessarily in laboratory experiments (e.g [1, 14]).

Though we might share similar patience levels with apes during some kinds of choices, we appear to have evolved a greater capacity for patience in other contexts (as indicated by the questionnaire responses). Why this difference emerged is not entirely clear. As study 3 demonstrates, reward type is one factor that influences preferences, and monetary rewards have many properties that distinguish them from biologically central rewards like food: They are storable, can be convertible into other reward currencies, might not be immediately rewarding in the same way that biological currencies are, and can take on extremely large values. Most studies of economic decision making involve choices about much larger amounts than those used in the iterated task, and reward magnitude influences human patience [20, 37]. Importantly, the concrete rewards used in animal studies must necessarily be small, and it is unclear whether any rewards of relevance to nonhumans could take on such large values. Furthermore, some level of temporal impulsivity might be evolutionarily favored in foraging contexts so that it could be ensured that organisms maximize their rate of gain [1, 14, 28, 38], but rate might not be a relevant currency for all decisions. In particular, total gains could be more important when making decisions about money—especially if the opportunity costs associated with waiting for money are typically low relative to the costs incurred when actively foraging for food.

The human participants' increased willingness to wait for money over food in study 3 aligns with previous results [19, 23] despite the use of very different paradigms. This suggests that the contrast between decisions about abstract rewards—or "cognitive" rewards—and decisions about basic rewards [12, 26] may be quite

robust. Notably, even limited exposure to money can systematically alter people's goals and behavior [39], and cognitive and basic rewards recruit overlapping [40] but possibly distinct [41] neural systems. As such, human preferences can differ depending on biological relevance: Decisions about money are not necessarily representative of all decisions. It is therefore essential to examine preferences across a wide range of contexts to fully understand both the evolutionary pressures shaping human choice and the cognitive mechanisms underlying decision making.

Experimental Procedures

Study 1: Temporal Preferences in Chimpanzees and Bonobos

Subjects

We tested five chimpanzees (8 to 30 years; three females and two males) and five bonobos (8 to 23 years; two females and three males), socially housed at the Wolfgang Köhler Primate Research Center in Leipzig, Germany. Apes had ad libitum access to water, were never food deprived, had access to food outside experimental contexts, and could stop participating at any time.

Procedure

Subjects chose between a small, immediate reward and a large, delayed reward (see Figure 1). Each session consisted of four introductory trials (forced choice with only one option available) for familiarization, and ten choice trials followed. The large rewards' delay was adjusted in a subsequent session according to a subject's preferences in the previous session (see the Supplemental Data). We determined each subject's indifference point by comparing the mean delay to large of their last five sessions with the mean delay to large of their previous five sessions (as in [6, 8]). Subjects were considered indifferent when these means differed by less than 10%. The mean delay of a subject's last five sessions was used as their estimated indifference point (see the Supplemental Data).

Study 2: Comparison of Patience in Humans and Chimpanzees

Subjects

We tested 19 chimpanzees (4 to 31 years; 13 females and six males) and 40 adult humans. Eighteen participants were from the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany (mean age: 27.7; eight females and ten males) and 22 were from Harvard University (mean age: 20.5; ten females and 12 males). These populations did not differ in an initial analysis (see the Supplemental Data), so they were combined.

Chimpanzee Procedure

Each chimpanzee completed three sessions per condition, with the same general procedure as study 1 (see Figure 1). For each condition, the first session consisted of 16 introductory trials. Subjects then completed two test sessions, each consisting of four introductory trials and then six choice trials. After approximately 1 week, subjects completed their second condition.

Human Procedure

Human participants completed one session, randomly assigned to condition. In advance, they were informed that the experiment would take up to 45 min, and asked to refrain from eating for the hour prior to the experiment if possible to ensure food motivation. After obtaining informed consent, the participant and experimenter (E) sat across from each other at a table. E read from a script (see the Supplemental Data), informing participants that they would first complete four "practice trials" (introductory trials), and then make a series of choices between the two options (six trials like the chimpanzees, although participants did not know how many in advance). Participants in the delay condition were not told the delay's duration, but experienced it in the practice period beforehand. Participants then selected their preferred food (raisins, peanuts, M&M's, Goldfish crackers, or popcorn). A glass of water was available throughout.

During introductory trials, E placed a cup on the table and asked how many items it contained (either two or six). In the control condition E said "You can now have the food" immediately after the participant responded. In the delay condition E said this immediately for the small reward, and after two minutes for the larger option.

E moved 3 m away from the subject to another chair during the delay. In test trials, E placed two options on the table (counterbalanced for side assignment) and said "Do you prefer this cup or this cup?" As with the apes, E removed the forgone option after the choice, participants could take as long as they wanted to eat the food, and a 30 s intertrial interval (ITI) began when they placed the last piece in their mouth.

After the food task, participants completed a questionnaire (see the Supplemental Data) including hypothetical discounting questions [20] and scales assessing hunger and food preference [25]. Fourteen additional subjects reported that they were not hungry or did not like the food, and were excluded from the main analyses to ensure that the food was rewarding for the humans. However, these individuals did not affect the main results (see the Supplemental Data).

Study 3: Human Patience and Reward Type

Subjects and Procedure

We tested a naive group of 20 participants from the Max Planck Institute for Evolutionary Anthropology (mean age = 27.6 years; 12 females and eight males). Participants completed one session identical to the delayed food condition but involving choices about money (two 10 cent coins versus six 10 cent euro coins; see the Supplemental Data). Subjects knew they could keep all money from the experiment, and were requested to transfer the money into another cup after E said "You can now have the money." The next ITI began when the participant finished transferring the coins. Subjects completed a questionnaire after the main task as in study 2.

Supplemental Data

Experimental Procedures, three tables, and two movies are available at <http://www.current-biology.com/cgi/content/full/17/19/1663/DC1/>.

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