Animal Cognition: Great Apes Wait for Grapes

Humans may be patient when it comes to money, but chimpanzees are willing to wait longer than humans for food, suggesting patience is neither innate nor uniquely human.

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According to the old proverb patience is a virtue, but is it uniquely human? After all, only humans save for retirement, invest in the stock market, and buy savings bonds. As animals do not use money, it might be argued that the human capacity for delayed gratification derives from the use of symbolic, fungible currency [1]. Yet even in the absence of hard cash, people plan for the future by planting crops rather than eating the seeds, and prepare meats and fish for long-term storage. Indeed, archeological records suggest that future-oriented behaviors like food storage that require delayed gratification developed by the end of the last Ice Age, if not earlier [2].

These intuitions about human patience are supported by decades of research in economics and psychology [3]. Study after study has shown that humans are several orders of magnitude more patient than most other animals. In a typical study of patience, subjects (human or animal) choose between a small reward offered sooner and a larger reward offered later [4–7]. The size of the smaller and larger rewards as well as the delay to delivery are varied to determine when subjects find them equally valuable — the so-called indifference point. For example, a typical person might find $100 now and $200 a year from now equally rewarding. From such data, scientists can construct a discount function that estimates the decline in value of a reward as a function of how long one must wait to obtain it [6]. Data from inter-temporal choice tasks such as this tend to show that humans have a very shallow discount function for monetary rewards and will wait weeks, months, or even years for a small increase in payoff [3].

By contrast, previous research has shown that nonhuman animals are much more impulsive than people (Figure 1). For example, rats prefer a small immediate reward to one that is twice the size but for which they have to wait eight seconds. Exercising even less self-control, pigeons impulsively prefer an immediate small reward if they have to wait only four seconds for the larger one [4]! No human would be indifferent to $100 now and $200 in eight seconds.

Differences in patience between humans and other animals are often thought to reflect intrinsic cognitive differences associated with language, culture and symbolic thought. According to this line of thinking, patience, or its converse, impulsiveness, is a biological trait, just like running speed or color vision, and is largely fixed within a particular species, including humans.

A new study by Rosati and colleagues [8], just published in *Current Biology*, however, suggests that the reality behind the intuitive *Scala Naturae* of patience may be more complex. They report the surprising finding that under some conditions nonhuman animals can be much more patient than humans. The authors studied how long hungry humans, common chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) would wait for a food reward (grapes for apes, and snack food like popcorn and M&Ms for humans). On each of several trials, subjects chose between an immediate small amount of food and a delayed large amount of food.

Not only were both species of apes much more patient than rats, birds and monkeys, but the chimpanzees were significantly more patient than the humans (Figure 1). While the majority of chimps would wait an extra two minutes for four more grape halves, fewer than 20% of humans would wait the same amount of time for four extra pieces of their favorite snack. These results show that apes can be quite patient and that we are not always as patient as we would like to think we are. The authors also found that bonobos would wait about 75 seconds for the extra food, making them less patient than chimps, but

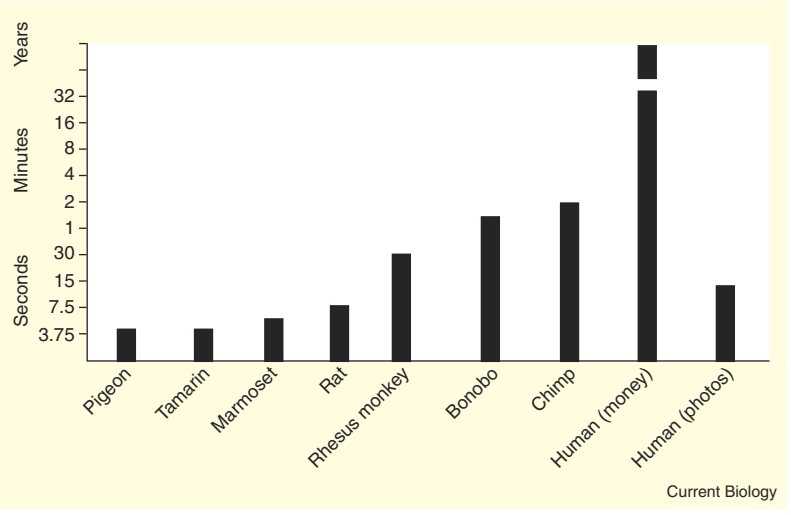

Figure 1. Patience in human and nonhuman animals.

Maximum estimated delay each species will wait for a food (or other) reward twice the size of an immediate reward is plotted on a logarithmic scale. Data for humans choosing amongst food rewards is not included because the parameter was not estimated. Data from [4,5,7,8,12].

substantially more patient than other animals.

Given the surprising outcome of the comparison between chimpanzees and people, Rosati *et al.* [8] were compelled to rule out other possible explanations for the results. For example, one might argue that people really just didn't care about the food reward and instead favored the instantaneous option to minimize the time spent in the experiment: however, the experimenters told the subjects that the experiment would take 45 minutes no matter what choices they made and all subjects were equally motivated as measured by the time taken to reach for the food. Alternatively, subjects may have simply been attempting to maximize their short-term reward rate [9]. To counter this proposal, the authors performed a careful analysis that took into account food handling times and time between trials to show that such a strategy would lead to much greater impulsivity than was observed.

A final possibility is that the human subjects who participated in this study were just plain more impulsive than people studied in previous reports. To address this issue, Rosati *et al.* [8] ran a control experiment in which humans chose between immediate and delayed monetary rewards. They found that people were much more patient when the rewards were money than when they were food. These results clearly show that temporal discounting depends strongly on reward type [5,10,11] and throw into question the generality of findings using a single experimental paradigm.

These results provide compelling evidence that some animals can be remarkably patient and that humans can be remarkably impulsive when waiting for food rewards. Moreover, these observations suggest that self-control may not be uniquely human and may have evolved in primates sometime before the divergence of humans and other apes some five to eight million years ago. More generally, these results suggest that patience itself is not a single biological trait, like running speed — nor is it a virtue. The capacity for self-control may instead be viewed as a cognitive adaptation that evolves in response to selective pressures favoring delayed gratification and may be differentially deployed in distinct behavioral contexts.

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Wnt Signaling: It Gets More Humorous with Age

In addition to its myriad of contributions in development, disease and regeneration, recent research implicates the Wnt/β-catenin signaling cascade in yet another biological process — aging. The latest role of Wnt uncovers new complexities and opportunities for modulating the Wnt/β-catenin pathway in regenerative medicine.

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Decreased stem cell function and a decline in tissue regeneration are hallmarks of aging. Although stem cell dysfunction may not cause aging, it may underlie the diminished regenerative response in aged animals [1]. Whether such stem cell dysfunction is caused by intrinsic changes in aged stem cells, changes in the extracellular environment, or both, is being debated. Two recent papers by Brack *et al.* [2] and Liu *et al.* [3] show that, surprisingly, Wnt activity is increased in aged serum and in a mouse model of accelerated aging. This increased Wnt signaling may contribute to stem cell dysfunction in aged animals.

Increased Wnt/β-catenin Signaling in Aged Mice

In order to study age-dependent changes in stem cell number and function, Liu *et al.* [3] utilized *klotho* knock out mice, which exhibit many age-related disorders as a result of accelerated aging [4]. Klotho is a transmembrane protein expressed in the kidney and